ABSTRACT

Title of Document: COMMUNICATING IN SOCIAL NETWORKS: EFFECTS OF REVERBERATION ON ACOUSTIC INFORMATION TRANSFER IN THREE SPECIES OF BIRDS

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In socially and acoustically complex environments the auditory system processes sounds that are distorted, attenuated and additionally masked by biotic and abiotic noise. As a result, spectral and temporal alterations of the sounds may affect the transfer of information between signalers and receivers in networks of conspecifics, increasing detection thresholds and interfering with the discrimination and recognition of sound sources. To this day, much concern has been directed toward anthropogenic noise sources and whether they affect the animals' natural territorial and reproductive behavior and ultimately harm the survival of the species. Not much is known, however, about the potentially synergistic effects of environmentally-induced sound degradation, masking from noise and competing sound signals, and what implications these interactions bear for vocally-mediated exchanges in animals. This dissertation describes a series of comparative, psychophysical experiments in controlled laboratory conditions to investigate the impact of reverberation on the perception of a range of artificial sounds and natural vocalizations in the budgerigar, canary, and zebra finch.

Results suggest that even small reverberation effects could be used to gauge different acoustic environments and to locate a sound source but limit the vocally-mediated transfer of important information in social settings, especially when reverberation is paired with noise. Discrimination of similar vocalizations from different individuals is significantly impaired when both reverberation and abiotic noise levels are high, whereas this ability is hardly affected by either of these factors alone. Similarly, high levels of reverberation combined with biotic noise from signaling conspecifics limit the auditory system's ability to parse a complex acoustic scene by segregating signals from multiple individuals. Important interaction effects like these caused by the characteristics of the habitat and species differences in auditory sensitivity therefore can predict whether a given acoustic environment limits communication range or interferes with the detection, discrimination, and recognition of biologically important sounds.

COMMUNICATING IN SOCIAL NETWORKS: EFFECTS OF REVERBERATION ON ACOUSTIC INFORMATION TRANSFER IN THREE SPECIES OF BIRDS

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2011

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PREFACE

This dissertation is the result of my research as a PhD student at the Departments of Biology and Psychology, UMD. It has taken the form of individual studies, which are introduced by a general literature review followed by a statement of my main research questions. The following provides a succinct overview of the rationale, questions, approach, and results addressed in this dissertation.

Acoustic communication in socially and acoustically complex environments is characterized by a variety of challenges that animals and their auditory systems strive to overcome to successfully interact with conspecifics. Some of those challenges are brought about by the accumulation of reverberation during the transmission of acoustic signals and their masking by ambient and transient background noise. As a result, concomitant spectral and temporal alterations of the sounds likely affect the transfer of information between signalers and receivers, a process that is pivotal for the stability and functioning of any communication system. More specifically, reverberant environments may limit the signals' transmission range or the 'active space' over which communication occurs and impair the reception of encoded information while also offering potentially useful cues for sound source localization. In my dissertation work I aimed at quantifying and understanding the perception of complex structural changes in acoustic stimuli as they become reverberated in the absence and presence of background noise. By using three species of small oscine and psittacine birds, my studies tried to assess the impact on successful communication in a reverberant multi-signaler

environment and reveal any adaptations of the birds' auditory system to deal with the potentially associated constraints and potentials. I chose to focus on reverberation as a major aspect of overall signal degradation in order to evaluate its isolated effect on biologically relevant acoustic stimuli independently from other habitat-induced acoustic changes.

Changes in the acoustic structure of sound signals that accumulate during sound transmission are routinely used to gauge different acoustic environments and to estimate the distance of a sound source. It is not known, however, to what extent these structural alterations can fulfill the purpose of evaluating an acoustic scene in this way, and which type of sound features changes contribute most to this ability. Therefore, my first two ***objectives*** were to quantify the auditory system's ability to *(a)* discriminate between and *(b)* categorize different amounts of reverberation with and without simultaneous background noise (**Study I** and **II**). I used two different psychophysical approaches to measure this ability in budgerigars, canaries and zebra finches. In order to identify perceivable reverberation differences (**Study I**), I used an Alternating Sound Task in which a change in a repeated background had to be detected. The focus here was on induced changes in amplitude and frequency patterns *within* the signal, disregarding echoes added to the signal in time. I chose this design to gain insight into the potential of within-signal changes to serve as possible cue to distance and the acoustic environment in addition to level differences and echoes that accumulate over distance. Different artificial sounds as well as natural vocalizations

of the three test species served as stimuli that were reverberated digitally using a computer-implemented algorithm and tested with and without simultaneous background noise. Selected natural vocalizations were also reverberated naturally by transmitting and re-recording them in a soundproof chamber containing reverberant objects. In experiments testing the *categorization* of overall amounts of reverberation (**Study II**), birds were trained to follow a GO/NOGO psychophysical procedure with selective playback options for GO, NOGO, and probe stimuli. They had to generalize across two large stimulus sets (reverberation categories) that each contained numerous hetero- and conspecific vocalizations and only differed in the degree to which they were reverberated (GO and NOGO level category). Randomly introduced new reverberated stimuli (Probes) had to be assigned by the birds to one of the two reverberation categories. For this task, tails of echoes were preserved, and six different category pairings were tested. ***Results*** showed that birds were able to hear even small changes in both naturally and digitally-induced reverberation, although this ability was somewhat dependent on both the species and, in particular, the type of signal (**Study I**). Broader-band natural and artificial signals and in some cases conspecific vocalizations posed the smallest difficulty compared to pure tones, although the non-oscine, flock-living budgerigar generally outperformed the other two oscine species (closely followed by zebra finches) independent of stimulus type and experimental condition. Tests with reverberated natural vocalizations whose fine structure was substituted with non-random white noise (retaining its reverberated amplitude envelope) revealed that envelope

changes alone were sufficient to detect even very little reverberation. Masking from white noise deteriorated listening conditions for all bird species and further decreased their overall sensitivity to sound alterations, although a strong synergistic effect between the two was not observed. Additionally, birds successfully *categorized* different amounts of reverberation across diverse stimuli, although this task was easiest at overall moderate reverberation, e.g. the level difference between two categories alone did not predict a bird's performance (**Study II**). Not surprisingly, however, performance was overall worse than in the discrimination task described above. Taken together the results of the first two studies suggest that although even minute reverberation differences could be easily discriminated, categorization proved more difficult, especially when birds had to categorize high amounts of reverberation. In summary, reverberation-induced signal alterations seem to provide distinguishable and potentially useful cues to distance and to the acoustic quality of the environment, but may be more important when communication distances are relatively short. Moreover, the question of whether such cues are indeed used still remains open.

In previous studies with humans, degradation brought about by artificially created room reverberations resulted in deteriorated speech segments and decreased speech intelligibility. Similarly, one of my earlier field studies on sound degradation in great tits (*Parus major*) indicated that similar song types, which are shared by neighbors, become yet more similar (and likely less distinguishable) when they are subject to habitat-induced degradation. Yet, subsequent behavioral field

experiments with nesting female great tits unequivocally revealed that females recognized their mate despite such high song similarity and sound-degrading conditions. The ***objective*** of my next study therefore was to investigate to what extent reverberation obliterates individually distinct acoustic features and hinders effective, vocally-mediated information on identity between signaler and receiver (**Study III**). Birds were tested in an Alternating Sound Task, in which a short vocalization from one individual was played repeatedly as 'background' and randomly alternated by a similar 'target' vocalization from another individual of the same species. Both background and target vocalizations were played back at eight different, randomly chosen degrees of reverberation. Again, tails of echoes were retained to allow for changes in signal duration. Three types of vocalizations per species were used in alternation: calls, single song syllables, and short song sequences. Experiments were repeated with two levels of a continuous, band-limited white noise masker to test the additional effect of ambient noise. ***Results*** suggest that, within the tested range of reverberation levels, discrimination between similar but individually distinct vocalizations became somewhat more difficult but not entirely impossible with increased amounts of reverberation. Only the combined effect of high reverberation and background noise considerably impaired discrimination and caused birds to guess more (while reverberation or noise alone did not). Budgerigar and zebra finch vocalizations with their more broadband character and higher levels of frequency modulation compared to canary vocalizations were generally easier to distinguish even under deteriorated

acoustic conditions, and seemed to retain some degree of individual distinctiveness in their overall pitch or other fine spectral patterns. Moreover, performance appeared to be species-dependent, with budgerigars once more outperforming the other two species, while canaries seemed to have the greatest difficulty. Since performance was in fact dependent on reverberation and noise levels I could exclude the possibility that birds had merely memorized or habituated to the repeating background of one individual's reverberated vocalizations. Instead, the results suggest that a decrease in performance was due to an increase in perceived similarity among individual renditions of the same vocalization, which bears important implications for species that exhibit song sharing or other forms of vocal imitation. Multimodal communication or mechanisms such as spatial release from masking could mitigate these effects in the wild.

In the context of individual discrimination, it was important to address the contributions of reverberation to the so-called *Cocktail Party Problem* in the analysis of an acoustic scene (**Study IV**). As in humans, animals that communicate in groups and social aggregations are faced with the problem of acoustic interference and informational and energetic masking from multiple biotic and abiotic sound sources as well as the scattering of sound waves in the environment. The resulting composite waveform at the receiver's end has to be parsed by the auditory system into separate, perceptually coherent sound components that represent different sound sources, a process known as *auditory object formation* or *stream segregation*. In the presence of many simultaneous signals individual discrimination

is hindered not only by the increased vocal similarity that reverberation causes (see **Study III**). It may also be affected by the auditory system's inability to separate vocalizations of one individual or species from those of others in the form of a separate auditory object. Although reverberation likely complicates auditory scene analysis, previous studies with birds *and* humans have used competing signals that were *not* reverberated but provided well-conserved grouping cues. Reverberation, however, may promote increased interweaving of sound waves and result in a potentially chaotic mix of smeared signals, in which otherwise distinctive auditory grouping cues are obliterated. The last ***objective*** of my dissertation project therefore was to test whether the auditory system's ability to parse a composite waveform into coherent auditory objects is compromised when a complex acoustic scene with multiple signalers contains reverberated signals. I again used a GO/NOGO psychophysical procedure in which birds had to be trained to listen to long sequences of natural vocalizations and wait to give final responses first after the end of playback. Test stimuli consisted of 4-s sequences of coherent natural vocalizations recorded from unfamiliar individuals of each of the three tested species. The GO stimulus consisted of the complete natural sequence, whereas the NOGO stimulus was made up of the same GO stimulus sequence with a minimal (mainly spectral, temporal or compositional) change towards its end. This forced the birds to attend to the entire sequence before making a response decision. The continuous background consisted of a 2-min loop of coherent songs from a varying number of other unfamiliar birds of the same species. ***Results*** clearly showed that

the birds' ability to selectively attend to a specific sequence of sounds was particularly compromised when very high reverberation levels coincided with many birds singing in the background, while many signalers or high reverberation levels alone did not have an effect of similar severity. In comparison with canaries and zebra finches, budgerigars had an overall easier time following a particular song sequence and discriminating it from others. This was true across all reverberation levels and vocalization types. These findings suggest that within the tested range of reverberation levels and number of simultaneous signalers, low and moderate reverberation do not interfere much with the receiver's ability to segregate or 'hear out' longer sequences of sounds from multiple individuals. At these moderate levels receivers can still detect and distinguish signalers despite degraded auditory grouping cues. More severe reverberation, however, limits this ability considerably.

Taken together, small amounts of reverberation do not necessarily pose great difficulty to the receiver in decoding important messages, especially if simultaneous masking from noise is low. Highly reverberant environments, however, appear to face the birds' auditory systems with increased perceptual challenges that require an adaptation to the acoustic dynamics of complex, multi-signaler environments to retain the ability to communicate successfully in all social contexts. According to the present results, the auditory system of the budgerigar seems to be a step ahead in solving the perceptual problem of listening to signals in reverberant, noisy environments. This may be reflective of the species' advanced cognitive flexibility or capacity that also enables the birds to learn large numbers of

new vocalizations throughout life, whereas canaries and zebra finches are so-called closed-ended learners who practically lose their ability to learn new songs after the end of a sensitive learning period. Therefore, a rich social environment (as seen in flock-living species such as the budgerigar) combined with the capacity to learn new vocalizations may help equip the auditory system with a perceptual flexibility that is necessary for the advanced perceptual task of communicating in social groups and sound degrading environments. Furthermore, my studies strongly imply that in order to fully understand the potentials and constraints of communicating in social groups, one must consider not only the acoustic properties of the signals and the masking noise, but also the physical make-up of the environment in which those signals are transmitted. Clearly, large amounts of reverberation pose a special problem to all receivers, particularly because their effect on communication strongly interacts with other factors, such as overall levels of biotic and abiotic background noise. Successful coping strategies require auditory systems to adapt quickly to dynamic changes in these conditions to either perceptually compensate or make use of some of the acoustic changes of the signals.

ACKNOWLEDGEMENTS

I would first and foremost like to thank my advisor, Bob Dooling, for his advice and great faith in my abilities throughout these past years. He has always made me feel welcome and valued, especially when I first crossed the Atlantic to be part of his lab. My committee has also been of invaluable help in shaping my ideas for this project. I thank Catherine Carr, Monita Chatterjee, Sandra Gordon-Salant, Art Popper, and Jerry Wilkinson very much for their input in both professional and personal matters, and for providing valuable comments and suggestions. Art Popper has been especially helpful in this regard. In addition to my advisor and committee, I wish to acknowledge many friends and colleagues I have gained over the years who have been of great help in their own special ways. Mounya Elhilali, Shihab Shamma provided some initial planning and programming help. I especially thank Ed Smith for providing technical support on so many occasions. He has been indispensable not only for solving technical problems but also for the many inspiring conversations we had. I am also very grateful to Beth Brittan-Powell, who has been a similarly good friend and colleague who would patiently listen, help solve problems and still see the funny side of things. I thank everyone in the lab for creating a great scientific and social environment, especially Bernie Lohr, my former fellow graduate students (Beth Vernaleo, Michael Osmanski, Isabelle Noirot**,** Vicky Tu, Kristina DeAngelo, and Amanda Lauer) and the various undergraduate students. Some of the undergraduate students were kind enough to run a few experiments when I had to teach. They made it a lot easier to juggle teaching and research, and I

am very grateful for their help. Most of all, I am grateful to David Eisner for being my most trusted friend and greatest support throughout my time as a graduate student in this odd country of his. More than anyone else he has given me a unique insight into American culture and lifestyle from a perspective that not every foreign national is privileged enough to experience. More importantly, however, he has kept me sane in many ways even during more trying times and has more than once been the 'light at the end of the tunnel' in my fights with programming codes and tedious analyses. Du bist klasse! Lastly, I would like to warmly thank my mother who has patiently accepted my choice to move even farther away after ten years in Denmark. Her love, understanding and support were crucial to fully enjoy this great opportunity to pursue my PhD education in the US.

My dissertation work was funded in part by the W. and M.T. Hockmeyer Research Fellowship for the Spring Semester 2010.

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1 INTRODUCTION – Basic Theories and Terminology

This brief introduction is written with the purpose of providing some general background for the ideas and questions that helped shape my dissertation research as well as to explain some of the terminology I will use repeatedly throughout this dissertation. It is not intended as an exhaustive literature review but merely as a summary of some of the current knowledge that formed the basis of my project.

1.1 The Behavioral Ecology of Animal Communication

Communication plays a central role in animal social life because it mediates important social interactions between conspecifics. It facilitates the formation and maintenance of relationships between mates, kin, and rivals within the group as well as between groups and populations (Dawkins 1995; Bradbury and Vehrencamp 1998; McGregor and Peake 2000). Most of us seem to have a very definite idea of what communication is about and what it entails due to our first-hand experience in everyday situations, in which we use speech to express ourselves. Defining animal communication on the other hand has been a subject of extensive debate over the past decades. One problem is that the definition of biological processes invariably requires us to consider a whole series of exceptions that are continuously provided by evolution and to stay away from the temptation to anthropomorphize these processes. Differences of opinion as to what should and should not be called communication largely center on quantitative considerations of how broad or restricted the definition should be. Another question is whether and to what extent

one should draw from sources in other fields, such as human communication (psychology) and information theory (mathematics), and how to combine the sources to ultimately reach a consensus.

In my dissertation I use communication to mean the process in which a signaler 'transfers information' to one or several receivers via a transmission channel using 'specially evolved signals'. This information then may or may not be used by receivers to make decisions about their ensuing behavior. (Dawkins and Krebs 1978; Dabelsteen 1988; Krebs and Davies 1993, 1997). I further employ the term 'information transfer' in a more colloquial sense than originally put forward by communication theorists, who emphasize the role of the external human observer as the receiver of transmitted information (Shannon 1948; Shannon and Weaver 1949), whereas my usage exclusively encompasses information transfer between senders and receivers that reduces the uncertainty about the sender's subsequent behavior. Moreover, I define 'signal' as any behavior available to an individual (sender) that has evolved through selection to transmit information and potentially alter the behavior of another individual (receiver) to the average benefit of the sender (Morton 1982; Slater 1983; Krebs and Davies 1997; McGregor and Peake 2000; Maynard-Smith and Harper 2003). I regard communication as a mutual exploitation, i.e. the outcome of both cooperation and conflict, between signaler and receiver bringing about a co-evolutionary arms race (Smith 1977; Krebs and Dawkins 1984; Smith 1997; see also review by Catchpole and Slater 1995) For communication to occur, at least two individuals must be involved – a sender and

receiver. Traditionally, signaling behaviors in animals have been studied from the perspective of communication 'dyads', while more recently the focus has shifted somewhat to communication within 'networks'. This is important, because many signals are long-range, i.e. transmit over long distances, and during their transmission these signals likely encompass several individuals, whether they are intended receivers or not. Put differently, signals have an 'active space', which is the sphere or hemisphere around the animal within which the sender can be detected by any available receiver (e.g. Brenowitz 1982; Bradbury and Vehrencamp 1998). As long as the average spacing among individuals is less than the maximum propagation distance of the signal, communication is said to occur in a network rather than being restricted to dyads (Dabelsteen 1992; McGregor 1993; McGregor and Dabelsteen 1996; McGregor and Peake 2000; McGregor et al. 2001; Peake et al. 2002; McGregor 2005). Therefore, the evolution of signals has to be viewed as taking place also in the context of communication networks and as a result of selection pressures that arise from vital network activities.

One intrinsic aspect of all communication systems (dyads and networks) regardless of signal modality, are the environmental constraints posed on them. Information is transferred only if the receiver is able to detect the presence of a signal and extract information from it (Shannon 1948). Signals of all modalities, however, are unavoidably degraded as they are transmitted from signaler to receiver. Signal degradation is the alteration of signal quantity (or strength) and quality and is caused by the medium through which the signal propagates. The

range of a signal is therefore limited by the properties of the medium and its boundaries as well as by the properties of the signal itself. Degradation does not only affect the detection of signals but also their intelligibility, which in turn determines whether or not a receiver can discriminate, recognize and extract encoded information from them (Shannon and Weaver 1949; Wiley and Richards 1978, 1982; Gerhardt 2002).

The diversity of signal designs and modalities that are used by animals in social information exchanges depends on, and is in part caused by, the constraints arising from the physical make-up of the environment and the physiological properties of the animal's sensory system. Therefore, answers to the question of which modality is most adaptive for a given species should be based on considerations regarding factors such as the signal's transmission range, directionality, durability, ability to go past obstacles, and the energetic costs resulting from its production. In fact, many behavioral contexts require a combination of several sensory channels to engage in effective communication and get the message across. (Krebs and Davies 1997; Bradbury and Vehrencamp 1998; Marler and Slabbekoorn 2004; Slabbekoorn and den Boer-Visser 2006)

The studies presented in subsequent chapters concern the effect of sound reverberation on specific acoustic communication aspects in birds. My general introduction will therefore continue with an explanation as to why so many animals, especially birds, are predominantly vocal in their interactions with each other, followed by a focus on acoustic signals and their degradation below.

1.2 Why Use Sound?

Sound is a common signal modality that is used across a wide variety of species. It can be costly to produce, but it has several advantages compared to other channels of communication, such as those of olfaction or vision. Sound transmits independently of diurnal light-dark cycles, and travels over potentially long distances. It can be adjusted by the signaler, is more or less omni-directional yet fairly easy to locate, and obstacles have a relatively low impact on the signal's propagation to a receiver. Another benefit is the rather fast and transient nature of sound signals. Their production is immediate and they only last for as long as they are produced. These advantages have come to outweigh the potentially high energetic cost associated with the production of the impressively large amounts of acoustic signals animals emit over the course of just one day. (e.g. Alcock 1989)

1.3 The Physics of Sound Degradation

Within sound signals information is encoded in the acoustic properties of the sound wave as well as its temporal pattern of delivery. A sound signal is thus uniquely characterized by its amplitude and frequency patterns over time, overall duration and duty cycle. Degradation, however, acts upon these properties and, as mentioned earlier, ultimately modifies the quantity and quality of the signal. The precise outcome of these alterations depends on both the signal structure and habitat characteristics as well as on the behavior of signalers and receivers. To clarify some of the complexities of the relationship between signal and habitat, I

will in the following sum up some of the major physical processes of sound degradation. The reader should bear in mind that in natural environments these processes do not occur isolated but act simultaneously and often synergistically, causing rather complex patterns of sound wave propagation. Note also the differential use of the term degradation in the literature. Some have used it synonymously with 'distortions' of temporal and spectral patterns alone, excluding changes brought about by attenuation (e.g. Morton 1975; Richards and Wiley 1980; Gish and Morton 1981; Wiley and Richards 1982; Waser and Brown 1986). I prefer to use it as a collective term for all alterations accumulating during transmission through the environment, a usage that has become increasingly more common (Michelsen and Larsen 1983; Michelsen 1992; Dabelsteen et al. 1993; Holland et al. 1998; Nemeth et al. 2001; Balsby et al. 2003; Blumenrath and Dabelsteen 2004; Lampe et al. 2007; Barker et al. 2009).

The following is based on several reviews and some direct experimental evidence from early sound transmission studies (Pridmore Brown and Ingard 1955; Evans et al. 1972; Morton 1975; Marten and Marler 1977; Marten et al. 1977; Piercy et al. 1977; Michelsen 1978; Wiley and Richards 1978; Roberts et al. 1979; Klump 1983; Michelsen and Larsen 1983; Cosens and Falls 1984; Embleton 1996; Bradbury and Vehrencamp 1998). I will therefore not refer to them individually below.

1.3.1 Attenuation

Attenuation is one of the major aspects of degradation. It affects the signals 'intensity' (previously also referred to as 'quantity') and thereby also its detection, discrimination, and recognition. It is brought about by spherical spreading, atmospheric absorption, scattering, and boundary interference. These four processes result in a reduction in the overall signal amplitude and a concomitant lowering of the signal-to-noise ratio, while the latter three produce frequency-dependent attenuation. In long-range communication, these three processes are therefore important factors that determine optimal frequency ranges for sounds produced in a particular habitat or in specific locations of that habitat and contribute to so-called 'sound windows'.

1. *Spherical Spreading* – In a homogenous environment with no boundaries intensity decreases inversely with the square of the transmission distance when the sound source is small ($1/d^2$, d = distance between signaler and receiver; 'inverse square law'), resulting in a reduction of 6dB per doubling of distance (abbreviated 6 dB/dd; 'inverse distance law'). This law only applies to omnidirectional monopole sound sources as well as to dipole sources when attenuation is outside the acoustic near field. Inside the near field, intensity reduction follows patterns that are much more complex, because the relationship between molecular movements and pressure is rather complicated and substantially influenced by minute changes in distance. In transmission studies, researchers often focus on the attenuation of signal energy in excess of

the 6dB/dd in the far field, i.e. the 'excess attenuation', assuming relatively omnidirectional monopole sound sources.

2. *Atmospheric Absorption* – Energy is absorbed as a sound wave passes through a medium, but it is often difficult to distinguish between absorption per se and other attenuating processes. Because of the viscosity of the medium, part of the kinetic energy of the sound wave dissipates as heat ('classical component' of absorption), whereas the other part is absorbed within the molecules of the atmosphere ('molecular component'). Absorption is a complex function of temperature, atmospheric pressure, relative humidity, and the propagated sound frequency. In air, temperature and humidity have counteracting effects, for example energy losses are greater at low relative humidity and at higher temperatures. In natural environments and over frequency ranges typically used by birds (approximately 1-10 kHz), absorption increases monotonically with frequency for any value of humidity and temperature. This then alters the sounds' frequency spectra. Yet, in temperate habitats the effects of changes in temperature and humidity usually cancel each other out, because they typically rise and fall together.
3. *Scattering* – The use of the term 'scattering' varies a great deal among authors. Generally, scattering is referred to as the process in which the pathway of a sound wave is altered and redirected by heterogeneities in the medium. I will in my dissertation use it as a term comprising multiple reflections, diffractions and refractions of sound waves, whereas in the literature it is often equaled only

with diffractions. Heterogeneities along the path can be physical obstacles (e.g. vegetation) as well as air turbulences and temperature gradients (see "Stratified media and non-flat surfaces" below). The resulting sound wave is produced by the interference between scattered (indirect) and the incident (direct) waves. This interference is complex and depends on the relation between scale or size of the heterogeneity and the wavelength of the sound. It is also influenced by the size of the source and the distance between signaler and receiver. The *amount* and *type* of scattering, too, is greatly dependent on the wavelength of the incident sound and the dimensions of the heterogeneities. Consequently, scattering, like atmospheric absorption, constitutes an important source of frequency spectrum filtering in any natural acoustic environment.

4. *Boundary interference* – Sound waves can be reflected also from boundaries in the vicinity of the pathway, including the ground. Here again, the propagating sound is affected by interference patterns of the direct wave and the indirect waves from the boundary. Interference is either constructive or destructive depending on the differences in path length, frequency, and the induced change in path length introduced at the boundary. This generally applies only to frequencies around 1-2 kHz. When waves of much lower frequencies are redirected from the ground, interference patterns are further complicated by interactions between waves propagating along and just above the ground (ground and surface waves, collectively called boundary waves). Because of the intermediate frequencies of most natural bird vocalizations in temperate

habitats, interference due to boundary waves should not occur. As for all interference phenomena, the acoustic properties of the surface, such as the porosity or acoustic impedance of the ground relative to that of the air, the angle of the incident waves the distance between source and receiver as well as their height are important in determining the characteristics of the sound field created near the ground. Like atmospheric absorption and scattering, boundary interference is frequency-dependent in that it accentuates some frequencies while attenuating others.

1.3.2 Distortion

Distortion is the second aspect of degradation that has a particularly high impact on the discrimination of signals at certain propagation distances. In contrast to attenuation, it alters the fine structure of the sound signal in both the frequency and time domain. Distortion usually does not strain the receiver in detecting a signal but rather in discriminating it from others, while attenuation always affects the receiver's ability to both detect *and* discriminate signals. The alteration of signal structure is brought about by two main processes: Accumulation of both reverberated energy and irregular amplitude fluctuations. However, frequency-dependent attenuation that results from the processes described above also contribute to the overall distortion, because these processes differentially affect the relative sound intensities in the frequency domain and thereby distort the spectral components of the signal.

1. *Reverberations* – Reverberations result from the scattering of sound waves during propagation. This effect is large in environments with dense vegetation, such as forests. The reverberated acoustic energy distorts the sound in the temporal domain, because it both overlaps and is added to the incident sound wave in time. As a result, the energy of the signal decays gradually and over a longer period of time, extending the overall duration of the sound. In forests this decay is roughly exponential. Reverberations therefore mask rapid amplitude and frequency modulations as they for instance are found in trills. The level of reverberation depends strongly on the frequency of the sound, the density and type of reflective surfaces, the transmission distance, and the directivity of the sound. Emissions from relatively omnidirectional sources (such as small birds), result in substantially greater reverberations.
2. *Amplitude fluctuations* – Irregular amplitude fluctuations can arise from non-stationary heterogeneities in the medium, such as a turbulent atmosphere or irregularly moving objects (e.g. leaves in the breeze). This effects is most prevalent in open habitats where the direction and level of air current varies considerably and randomly even on calm, windless days, although in forests such amplitude fluctuations due to wind can become quite appreciable, too. The number of added modulations increases with sound frequency, propagation distance, and the dimensions of heterogeneities such as eddies and non-stationary objects, but decreases with a sound's increasing modulation rate. In contrast to reverberations, distortions by turbulence thus mask low rates of AM

and are usually negligible for modulations larger than about 50Hz. Changes in modulation rates result in added sidebands above and below the carrier frequency of the emitted sound, producing an exponentially decreasing envelope of side bands. Due to the temporal resolution of the average bird auditory system of only about 50 ms, however, fluctuations in amplitude caused by air turbulence are predominantly perceived as variations in intensity.

1.3.3 Other Impacts on Sound Reception

1. *Stratified media and non-flat surfaces* – The speed of sound is dependent on temperature, the medium's composition and pressure, and the degree of mass flow (such as wind). In air, there are often vertical temperature and wind speed gradients that lead to corresponding gradients in sound velocity above the ground or vegetation. Sound passing through a stratified medium is successively refracted into zones of lower velocity. For instance, sound fields are bent downward in a temperature inversion or for downwind propagation. Upwind or in a temperature lapse, however, sound waves are refracted upward, creating a shadow zone or 'sound shadow' into which only little sound energy is transmitted via creeping waves. In forests with foliage, temperature gradients are usually formed exclusively above, or from above to below the canopy, both resulting in sound 'channels' or 'wave guides' below the canopy. The effects of micrometeorology near the ground are similar to effects of non-flat ground surfaces. This means that temperature inversions and lapses are analogous to surfaces that are curved upward and downward, respectively. Velocity gradients

are one of the contributors to scattering of sound waves (see above), and their effect is therefore frequency-dependent. Low frequencies are much less affected, and for frequencies below 200 to 400 Hz sound shadows are in fact not formed at all.

2. *Ambient background noise* – The level of masking background noise ultimately determines the range at which sound signals are detectable. In fact, it has a stronger effect on the best frequency for communication than hearing. Both physical processes (wind, rain, breaking waves) and biological processes (other vocalizing animals and anthropogenic noise) can produce a more or less continuous background sound that spans over a wide range of frequencies. Ambient abiotic and biotic noise levels in natural environments can be quite substantial and play an important role in masking sound signals. In terrestrial habitats, one can find a rather quiet window between 1 and 4 kHz. Below that range, noise is predominantly produced by wind and air turbulences (below about 2 kHz), while sounds produced by some animals, like chorusing insects, are a source of high-frequency noise above 2 kHz. In temperate habitats, however, masking from vocalizations is less severe than in tropical habitats because it is not continuous and instead frequently provides temporal gaps in noise that allow for 'dip listening'.

1.4 Habitat Differences and Signal Design

A substantial body of evidence on the acoustics of natural environments comes from a large number of transmission studies that were conducted in different types of habitats (e.g. Morten 1975; Marten and Marler 1977; Marten et al. 1977; Richards and Wiley 1980; Cosens and Falls 1984; Price et al. 1988; Dabelsteen et al. 1993; Halland et al. 1998; Balsby et al. 2003, Blumenrath and Dabelsteen 2004 to name just a few). Not surprisingly, these studies collectively demonstrated that sound degradation varies considerably among habitats. Very early on, E.S. Morton (1975) formulated the 'acoustic adaptation hypothesis' for birdsong. According to this hypothesis, commonly used vocalizations should be structured in such a way that they are degraded least and transmitted over the longest possible distance. But with the many different experimental approaches, the diversity of test signals and studied habitats (or even patches within a particular habitat) it is still somewhat difficult to draw any more widely applicable conclusions as to the relation between habitat-induced degradation and concomitant signal adaptations. What these studies have unequivocally shown, however, is that it is a rather complex interface. As a rule of thumb, for maximum efficiency of long-range communication, the use of low frequencies reduces attenuation by differential absorption (Morton 1975; Wiley and Richards 1978, 1982). For sounds travelling near the ground, however, there is a lower limit to low frequencies as it otherwise results in destructive interference (see above). Many studies have reported that average best frequencies differ between habitats, especially in the tropics (Chapuis 1971; Morton 1975).

Another factor restricting the range of optimal frequencies are the reverberations that are caused by scattering of sound waves from multiple surfaces (e.g. vegetation). Reverberations are particularly strong in dense habitats such as forests, whereas in open habitats amplitude fluctuations are the major source of signal distortion. Vocalizations used by forest-living animals should therefore be relatively low in frequency and with few or only slow rates of syllable repetition and amplitude and frequency modulation. Comparisons within the same species of groups inhabiting different environments, such as the great titmouse *Parus major*, have shown that songs indeed have a lower average frequency and are overall much more tonal in forest habitats than in open woodlands (Hunter and Krebs 1979; Roberts et al. 1979; Slabbekoorn and den Boer-Visser 2006).

It is important to bear in mind that environmental selection on acoustic structure is only one of many selective forces that may shape communication systems and the vocalizations animals produce. Morphological constraints of the vocal production system/apparatus as well as of the auditory sensory system often stand in stark contrast to the selection pressure resulting from the properties of a specific habitat. Another cautionary note concerns the species' history in terms of the phylogenetic pattern of the produced vocalizations. Not all signal variation we see within a species is the outcome of an evolutionary adjustment to its natural environments but can be explained by an extensive variation among the species' ancestors. The used sounds may in fact not merely characterize one species but a larger monophyletic group.

Ryan and his colleagues (1985, 1990) give a brief review of the selective forces and the constraints imposed on evolution in communication systems and on a trait's ability to respond optimally to a given selective force. Furthermore, we shall see later that maximizing the transmission range of signals may not always be the ultimate aim in all communication behaviors. Indeed, there are examples of bird vocalizations that are designed to exploit the effects of degradation to serve specific communication purposes (refer to "1.5.3 Facilitated Network Activities" for more details).

1.5 The Biological Challenge

So far I have described environmentally induced acoustic degradation from a physical viewpoint. But how do such sound alterations ultimately affect the behaving animal in its natural environment? Which activities in a social network of communicating individuals are constrained? Are there any activities that are in fact facilitated by or may even depend on degradation that is specific to a particular environment? How do animals then avoid, exploit or compensate for this process? To answer these questions I will now turn to the biologically relevant aspects of sound degradation. Since this dissertation presents studies on the perceptual implications of reverberation in three species of small birds, my emphasis in the following section will be on birds and bird vocalizations. I will begin with a brief outline of the functions of birdsong and the information it may encode to provide a better understanding of why the questions stated above are indeed relevant. I will

then continue with a closer look at the constraints imposed on communication in social networks, followed by a summary of the potential benefits arising from signal degradation. The latter will return to the previously discussed topic of adapted signal designs ("1.4 Habitat Differences and Signal Design"), this time from the perspective of degradation *benefits* to communication, and characterize the degradation-induced acoustical sound features that may aid distance estimation. I will also outline the strategies by which some animal species have shown to utilize these features to determine the location and direction of a particular sound source.

1.5.1 Birdsong – Functions, Contents, Ecology, and Terminology

1. *Functions* – Song has a variety of functions and facilitates recognition at many different levels. In many *oscine* bird species (songbirds), males do most of the singing. Their singing activity is partially controlled by the hormone testosterone, which induces high levels of singing at specific daytimes, predominantly during spring. Because many male songbirds occupy and defend a breeding territory, one main function of birdsong is to proclaim and defend a territory against rivals and intruders and can therefore be a highly aggressive signal. The other is to attract and stimulate potential mates as well as to form and maintain pair bonds, which are important in both songbirds and non-songbird (e.g. Thielcke 1970; Kroodsma and Byers 1991; Catchpole and Slater 1995; Farabaugh and Dooling 1996; Kroodsma and Miller 1996; Searcy and Beecher 2009). Birdsong can thus be said to have two main functions, one being *intra*-sexual and the other *inter*-sexual. It is worth noting, however, that it has

been difficult to show that this dual function of birdsong is generally applicable to a wide range of different bird species, oscine and non-oscine. Some of the available evidence is reviewed by Kroodsma and Byers (1991).

2. *Contents* – Song has been found to facilitate recognition at the level of species, populations, groups within populations, gender, kin, members of flocks, mate, and even territorial neighbors or strangers (Bretagnolle 1996; Farabaugh and Dooling 1996; Hailman and Ficken 1996; McGregor and Dabelsteen 1996; Ratcliffe and Otter 1996; Stoddard 1996). It can also contain information regarding the singer's state (age, fitness, paring status, and motivation), its location, and its potential ensuing behavior. In these cases, the transmitted information refers to the signaler itself and the signals are said to have internal referents. In contrast, signals with external referents (e.g. bee dance) contain information about external events or objects that are prevalent in the signaler's surroundings (Dabelsteen 1988; Dabelsteen and Pedersen 1988). The coding of this type of information in song requires a certain degree of complexity, which in some cases may conflict with the need for optimal transmission. Common encoding song parameters are song or note length, tonality as well as frequency and amplitude modulation. Song complexity and syntax as well as the duration of intervals between notes, phrases or songs might also provide information. In some bird species, even the size of and the variation within song repertoires can reveal a singer's identity (see reviews by Falls 1982; Hailman and Ficken 1996). The strength with which selective forces act upon signal evolution probably

depends on the importance of the specific information given (Becker 1982). The physiological properties of the sensory systems of both senders and receivers are thought to have great impact on overall signal design as a result of the co-evolution of coding and decoding strategies (Brackenbury 1982; Dooling 1982; Ryan and Brenowitz 1985; Ryan et al. 1990). As mentioned earlier, however, the properties of the transmission channel and thereby the habitat through which the signal travels might be equally important in shaping signal structure (e.g. Morton 1975).

3. *Ecology* – Although the use of acoustic signals poses a great advantage in communication across large distances and in environments with many physical objects, sound transmission between signaler and receiver still has its limitations. As mentioned in 1.4 "Habitat Differences and Signal Design", sounds are progressively distorted and attenuated the farther they travel (due to e.g. reflective surfaces and air turbulences). Moreover, all vocalizations are usually accompanied by an incessant cacophony of other sounds from various types of biotic and abiotic sources. To understand the ecology of birdsong one has to take a closer look at how signals change on their way from a sender to a receiver dependent on the acoustic environment, and to what extent the perception of these signals is additionally affected by the amount and type of ambient background noise that is specific to a certain habitat. More details pertaining to birdsong ecology are provided below (1.5.2 and 1.5.3).

4. *Terminology* – Traditionally, bird vocalizations are divided into two main, albeit arbitrary, categories: songs and calls. Most commonly, *songs* are long, complex sequences of vocalizations that are mainly produced by males during the breeding season, whereas *calls* are generally shorter, less complex and usually produced by both males and females throughout the year. Another distinctive feature between the two is that songs tend to be produced spontaneously. Calls, on the other hand, are produced under specific circumstances, such as fights, alarms, and other conflict situations, and are therefore much less spontaneous. Obviously, this distinction is not always clear-cut, and there are instances of vocalizations that fall somewhere in between the two categories. Because songs are often complex, they can be further divided into units, i.e. distinct, visually and acoustically recognizable sections. The largest units within a song are *phrases*, which in turn can be split up into *syllables*. These syllables occur together in a particular pattern and are therefore recognized as part of one specific phrase. At the beginning or end of a song, however, one can occasionally find start or end phrases, which are composed of units that do not share a common feature but are all different. The syllables themselves vary in complexity and can even be composed of several, yet smaller components referred to as *elements*. Elements are the smallest units of song and are basically defined as sounds that are represented as one continuous line on a sonogram. Some of the distinction between songs, phrases, and syllables can also be made by the duration of the silent interval between them. The largest

pauses are between entire songs, i.e. 'inter-song intervals', followed by inter-phrase intervals, and so on. Lastly, birds are also said to have song *repertoires*, which are collections of different song versions or song types that a bird chooses from during a singing bout. These repertoires can contain anywhere between one and several hundred different song types, and their composition is individually distinctive. Examples at both extreme ends would be the white-crowned sparrow *Zonotrichia leucophrys* or the ovenbird *Seiurus aurocapillus*, which have only one song in their repertoire, and the brown thrasher *Toxostoma rufum*, whose estimated repertoire contains more than 1500 song types. (Catchpole and Slater 1995; Lambrechts 1996)

1.5.2 Constrained Network Activities

Animals communicate in networks of conspecifics in a wide range of biological and behavioral contexts, such as territory defense and mate attraction (McGregor 1993; Catchpole and Slater 1995; Kroodsma and Byers 1991; Ratcliffe and Otter 1996). There is ample experimental evidence to suggest that these networks provide unique opportunities for animals to acquire social information from the behavior of others (McGregor and Dabelsteen 1996; Giraldeau 2002; Dabelsteen 2005; McGregor 2005; Peake 2005), with information on individual identity being particularly important to a dynamic, well-functioning network of conspecifics (Farabaugh et al. 1994; Farabaugh and Dooling 1996; Dabelsteen 2005; McGregor 2005). Communication behaviors in social networks thus can have important fitness consequences, especially in the context of sexual selection and species recognition

(Becker 1982; Bradbury and Vehrencamp 1998; Gerhardt 2002; McGregor 2005). Aside from providing unique opportunities for social information exchange, communication in large networks or groups also has its own unique challenges. The presence of multiple signalers complicates the overall acoustic scene, in that the acoustic signals of several individuals often occur concurrently and in addition to ambient noise from abiotic and biotic sources (including signals from other species) (Klump 1996b; Hulse 2002; e.g. Brumm and Slabbekoorn 2005; Bee and Micheyl 2008). Signals are therefore often overlapped in frequency by other sounds which causes *energetic* masking of the signals. Additionally, even vocalization components that do not have the same average frequency but merely overlap the signal in time are a ubiquitous source of *informational* masking (e.g. Kidd et al. 1994; Durlach et al. 2003). Such interference and masking consequently increases detection thresholds and complicates discrimination between different variations of signals. There are various ways by which the auditory system appears to have at least partially solved this challenge. With additional environmentally-induced degradation, however, communicative exchanges between animals over a large communication range are further limited (Morton 1975; Chapuis 1971; Michelsen 1978; Wiley and Richards 1978, 1982; Dabelsteen 2005).

Information can be gathered in a variety of ways, e.g. from eavesdropping on the signaling interactions of other individuals ('social eavesdropping'), or from intercepting the signals intended for another individual ('interceptive eavesdropping') (McGregor and Dabelsteen 1996; Otter et al. 1999; McGregor and

Peake 2000; Mennill et al. 2002; Tobias and Seddon 2002; McGregor 2005; Otter et al. 2005). Animals may also use public information (Valone and Templeton 2002) or other socially acquired information that may result in 'informational cascades' as e.g. seen in many flock-living animals (Giraldeau et al. 2002). Many of the vocally-mediated activities in networks thus involve encoding and extracting information, addressing particular receivers, privatizing or publicizing information, and localizing signaling individuals. Seen from the sender's perspective, degradation limits communication range and the directivity of the emitted signal, whereas on the receiving end, it affects the perception and decoding of the signal as well as locating its source. The ability of senders, direct (intended) receivers, and eavesdroppers to participate in the aforementioned and other network activities is therefore limited and may result in communication mistakes that may decrease fitness substantially. Therefore, factors contributing to this limitation have to be counteracted, if the aim is to maximize the transmission distance and intelligibility of the vocalization, and if the available sensory information is to serve behavioral control. Those mechanisms can be both physiological and behavioral. Physiological mechanisms involve the production (sender) and sensory processing (receiver) of sounds, while behavioral strategies involve the active adjustment of signaler or receiver behavior (e.g. via the choice of perches) to decrease degradation during signal transmission. For proper interpretation of transmitted information the auditory system has to be able to make quick but reliable perceptual evaluations. In contexts like the ones described above, it is constantly faced with the challenge of processing complex and dynamic

sensory input at first 'glance', if signals are not repetitive nor provide redundancy in some other fashion. This is particular challenging when degraded sensory information conveys a seemingly contradictory, incomplete or otherwise degraded/obliterated picture about an animal's surroundings. The auditory system must therefore follow organizational principles that help process received sensory information in biologically meaningful ways. Because acoustic communication activities seem to effectively take place in sound-degrading network environments on a daily basis, one could expect the auditory system to be sufficiently equipped with mechanisms that can make sense of an auditory scene that comprises degraded signals.

1.5.3 Facilitated Network Activities

Many bird species, like humans, are able to judge the distance to and direction of a sound source by attending to the received version of the sound. In particular, degradation of signals that accumulates over the propagated distance allows listeners to extract information about the sender's distance, an activity commonly termed 'ranging' (e.g. McGregor 1993, 1994; Klump 1996a; Naguib 1996b; Nelson and Stoddard 1998; Naguib and Wiley 2001a). In many social contexts, such information can be critical to both sender and receiver, and one might expect selection to favor long-range signals that are somewhat susceptible to degradation (preferably in a predictable fashion) while retaining other important information. Distance estimation of a sound source is thought to be a two-step process that requires an assessment of the degree of signal degradation and a comparison with

a reference or template that properly reflects the non-degraded state of the signal at its source (Morton 1982; Morton 1986; Shy and Morton 1986; Morton 1998; Naguib 1998; Wiley 1998).

The modified sound structure (e.g. Holland et al. 2001a, b; Mathevon and Aubin 1997), but also the change in sound pressure level or amplitude (e.g. Naguib 1997b; Nelson 2000) seem to provide distance cues to the receiver that can be used in ranging. Field transmission experiments with wren *Troglodytes troglodytes* song suggest that potential distance cues might lie in the energetic pauses (i.e. silent intervals) of the transmitted song (Holland et al. 2001a, b). The length of these pauses depends on the amount and relative time of arrival of reverberated energy, resulting in 'tails' of echoes. Others have suggested that location-specific rather than signal-specific cues (such as the direction of off-axis and near-axis reflections) may be used by birds independently of any knowledge about the acoustic behavior of the perceived signals in a particular environment (Nelson and Stoddard 1998). Because signal degradation appears to provide different types of potentially useful distance cues, it can be regarded as contributing to information transfer at some level. In cases where the sender benefits from being ranged, such as in territorial defense and mate attraction, its vocalizations should therefore have features that change predictably with distance even under variable acoustic conditions. Animals could essentially incorporate features in their vocalizations that aid the perception of degradation and the estimation of the corresponding source distance. Broad spectral components would make frequency-dependent attenuation more

detectable, and fixed temporal spacing between rapidly repeated notes (e.g. trills) would assist in the evaluation of reverberation.

In humans, there has been a long tradition for research on auditory distance perception (von Békésy 1938; Coleman 1962, 1963; Mershon and King 1975; Mershon et al. 1981; Min and Mershon 2005), but it has not received much attention in the discussion of communication in other animals. Most of the human studies have focused on the mechanisms of distance perception, which have proven difficult to assess in animals when these are tested in the field. Humans seem to be able to use reverberation, relative attenuation of high frequencies, and overall amplitude as cues to distance, indicating that only one of these cues is sufficient in distance estimation and may be processed separately (reverberation: (von Békésy 1938; Coleman 1962, 1968; Mershon and King 1975; Mershon and Bowers 1979; Mershon et al. 1989; Little et al. 1992). Interestingly, reverberation-induced signal changes have shown to be the only feature that can be used as an absolute cue in addition to serving as a relative cue. Both amplitude and frequency-dependent attenuation merely provides relative information regarding the distance of a source, i.e. in comparison with another sound. Some of the features listed here, however, are changes in the temporal and intensive characteristics of the acoustic stimulus brought about by diffractions of sound waves from the head and its external ears and by other so-called binaural cues that provide information about the actual locus of a sound relative to the head (i.e. distance *and* direction), and not just its distance (Coleman 1963; Carlile and Pralong 1994; Brungart and Rabinowitz

1999). Such binaural cues are particularly important if the sound source is not equidistant from both ears (i.e. is outside their midline). Directional information is of course also important in animals, although binaural cues are somewhat controversial and seemingly less important in animals with small head sizes, such as birds (Klump et al. 1986; Park and Dooling 1991; Klump and Larsen 1992), unless special adaptations exists (Konishi 1973; Carr and Konishi 1990; Konishi 1993). In birds, it may be mainly pressure gradients across the interaural canal (a tube that connects the left and right ear in birds) or pressure differences between interaurally decoupled ears (decoupled pressure receivers) rather than sound structural changes that provide binaural cues (Klump and Larsen 1992).

Another instance of beneficial degradation are situations in which the signaler may be interested in 'privatizing' communication between itself and a target individual and thereby preventing others to intercept the exchange (Dabelsteen et al. 1998; Dabelsteen 2005). Such situations often arise in territory defense, courtship, or predator alarms when the aim is to selectively target nearby individuals while excluding others. In situations where close cooperation between animals is pivotal, signalers may therefore choose signals with features that are particularly prone to degradation over distance, are transmitted and received poorly at long range, but retain some degree of directionality. This phenomenon can be observed in several bird species (reviewed by Dabelsteen et al. 1998) and is often referred to as 'cost-minimizing conspiratorial whispers' (Dawkins and Krebs 1978; Krebs and Dawkins 1984). For example, males of the European blackbird

Turdus merula, the yellowthroat *Geothlypis trichas*, dunnocks *Prunella modularis*, the alpine accentor *Prunella collaris*, the European red robin *Erithacus rubecula,* European redwing *Turdus eliacus*, and the dark-eyed junco *Junco hyemalis* often engage in 'quiet singing' (Ritchison 1995; Langmore 1996; Dabelsteen et al. 1998; Titus 1998), and in great titmice *Parus major*, both sexes are known to utter so-called 'zeedling' calls during courtship (Gompertz 1961). In other intersexual contexts, males may also simply reduce the amplitude of their full song (Lind et al. 1996; Blumenrath et al. 2007).The song of blackbirds *Turdus merula* and blackcaps *Sylvia atricapilla* contains low-pitched, tonal sequences with rather constant frequency (called motifs), and high-pitched, modulated twitter sounds (Dabelsteen 1984; Dabelsteen and Pedersen 1988; Mathevon and Aubin 2001). The 'zeedling' calls of great titmice have the same structural differences compared to full song as have twitter and motif sounds in the aforementioned species. Twitter sounds degrade considerably more over distance than motif sounds (Dabelsteen et al. 1993; Mathevon et al. 2005), and it is suggested that, at least in blackbird song, motif sounds are used in long-range communication and predominantly contain information on species and individual identity. Songs containing only twitters on the other hand seem to provide information on, for example, ensuing behavior and degree of arousal in addition to species identity, and may be used mainly at short range (i.e. in 'quiet singing'). (Dabelsteen 1984; Dabelsteen and Pedersen 1988, 1992) Furthermore, their rather directed pattern of radiation compared to motif sounds may help to successfully target the intended receiver (Larsen and

Dabelsteen 1990). If a bird wishes to 'privatize' its communication, it should thus use low amplitude signals that incorporate certain degradable features, such as trills with a high repetition rate, or broadband, high-pitched directional sounds with high rates of amplitude and/or frequency modulation (Wiley and Richards 1982; Larsen and Dabelsteen 1990; Dabelsteen et al. 1993). Moreover, the choice of relatively low perches or daytimes with high background noise levels could also be part of a privatization strategy, because both result in a decreased detection and discrimination range (Dabelsteen et al. 1993; Dabelsteen and Mathevon 2002; Blumenrath and Dabelsteen 2004; Dabelsteen 2005; Mathevon 2005). Similar strategies may be applied, if a sender seeks to conceal its identity (e.g. in lost territorial disputes).

2 PROJECT RATIONALE AND INTRODUCTION TO STUDY SPECIES

2.1 Outline and Objectives

Some animal studies concerned with environmental adaptations to the acoustic environment have looked at overall signal degradation that accumulates during transmission from a signaler to a receiver rather than considering each contributing effect alone. Some aspects of degradation such as frequency-dependent attenuation, reverberations, and amplitude fluctuations, however, have very distinctive, separate effects on the sound waveform, particularly its spectral and temporal fine structure. From a sensory system's perspective, the ability to process signal degradation is likely dependent on the frequency and temporal resolution of the tested auditory system. For instance, it is safe to assume that the degree of frequency resolution positively correlates with an animal's ability to hear spectral changes brought about by frequency-dependent attenuation. High temporal resolution on the other hand should make it easier for the receiver to judge levels of reverberation and differences in amplitude fluctuations. It is therefore important to separate these effects if the goal is to understand potential evolutionary effects of degradation on acoustic communication strategies.

In the light of these considerations, I decided to center my dissertation work on the perceptual consequences of communicating in reverberant environments. Reverberations are ubiquitous and known to deteriorate speech segments and adversely affect speech intelligibility in humans, including elderly listeners (e.g. Harris and Reitz 1985; Harris and Swenson 1990; Helfer and Wilber 1990; Helfer

1992; Gordon-Salant 1995). Obviously, sound reverberations are also prevalent in every-day communication in animals, and effective intra-specific communication plays a fundamental role in the conservation of many animal species. It is therefore highly significant to quantify and understand the perception of complex reverberation-induced signal changes and their impact on successful communication in animal species other than humans. It is furthermore important to understand the potential adaptations of the auditory system to deal with the associated constraints and potentials. Yet, controlled lab experiments investigating reverberation effects on animals are so far lacking, and hardly anything is known in depth about the perception of reverberated vocalizations in animals, the combined effects of reverberation, background noise, and competing sound signals, and what implications such deteriorated acoustic conditions bear for social recognition and other types of information transfer.

On the basis of the theoretical considerations described in the previous chapter (Chapter 1), the following questions emerged regarding sound reverberation and its effects on social information exchanges in multi-signaler environments:

1) Perception of differences in reverberation – *Study I*

- How sensitive are birds to subtle signal alterations that are brought about by reverberation?
    a. Is this sensitivity affected by ambient background noise?

b. Does signal type have an impact on the perceivable reverberation differences, and is the performance further species-dependent?

c. Are changes in the amplitude envelope alone sufficient to perceive reverberation-induced differences?

2) Categorization of reverberation across natural vocalizations – *Study II*

- Can different degrees of reverberation be categorized across various types of vocalization?

  a. If so, is extensive familiarity with the sounds at the particular amount of reverberation pivotal for correct categorization?

  b. Are there any species differences in performance?

3) Discrimination of similar, reverberated vocalizations from different individuals – *Study III*

- Does reverberation affect the discrimination of similar vocalizations of different individuals? In other words, can individually distinctive cues be preserved even when reverberation is high?

  a. Do background noise and reverberations have synergistic, deteriorating effects on the perception of these differences?

  b. Can birds discriminate better between similar yet reverberated sounds when these stimuli are conspecific rather than heterospecific vocalizations?

4) Auditory scene analysis in reverberant multi-signaler environments – *Study IV*

- Does reverberation affect the formation of auditory objects when the acoustic scene contains multiple signalers? In other words, can a target sound source be separated from several other sound sources when reverberation is high?
    a. Are reverberation effects dependent on the number of simultaneously vocalizing individuals in the background?
    b. Is the segregation of sound sources more effective if the sounds are conspecific rather than heterospecific vocalizations?

The questions addressed in this study are complimentary in their attempt to quantify the potential effects that reverberant environments may have on the communication behavior in social groups and networks. My approach uses simple study systems and reverberation models that let me manipulate experimental conditions in a highly controllable manner. The focus is on modeling reverberations and the signal distortions caused by time of arrival differences between direct and reflected waves. I further take a comparative approach that integrates questions from behavioral ecology with those from animal psychoacoustics using three species of domesticated birds as model systems. Comparisons are made across orders of vocalizing birds to establish potential species-specific adaptations. As test species, two oscines (songbirds), the canary (*Serinus canarius*) and the zebra finch (*Taeniopygia guttata*) were used as well as the budgerigar (*Melopsittacus undulatus*) as a psittacine (or non-oscine) species.

2.2 Introduction to Study Species

2.2.1 Why Study Birds?

Birds communicate in socially complex networks and are dependent on sound for the transmission of information regarding e.g. species, gender, identity, intentions, and status. They use various types of signals such as songs and calls to communicate over short and long distances and successfully inhabit all kinds of acoustic habitats, from dense forests to vast open plains and even urban areas with high levels of anthropogenic noise. In addition, the various breeding systems found among bird species ask for differential uses of vocalizations depending on whether the species is mainly territorial, non-territorial or colonial. Birds therefore offer a great opportunity to study how natural selection may have 'shaped' both signal structure for optimal transmission and auditory system function for reliable, uncompromised perception of these signals. On many levels, birds greatly resemble humans in their strong reliance on acoustic signals for communication in socially and physically complex environments. It therefore makes them suitable model species that have intrigued researchers for decades. In lab and field studies, birds have successfully served as models for elucidating the evolution, function, and underlying mechanisms of vocal communication (Dooling 1982, 1991; Catchpole and Slater 1995; Kroodsma and Miller 1996; Marler 2004; Marler and Slabbekoorn 2004; Zeigler and Marler 2004) and are particularly suited to investigate the impact of degradation on vocal communication in an evolutionary and ecological context (Catchpole and Slater 1995; Dabelsteen 2005). As previously mentioned, the songs

of many songbirds have the dual function of territory defense and mate attraction and thus have to serve both long-range and short-range communication, while flock-living, non-oscine, species (such as budgerigars) may use sounds mainly over short distances. Moreover, birds can produce a large diversity of vocalizations with different spectral and temporal features that are sufficient for individual or species recognition. The auditory system of many birds and their use of sounds in communication behaviors are well-investigated and provide considerable background knowledge (Dooling 1991; Dooling et al. 2000a; Dooling et al. 2000b), from which to address the research questions posed here. For instance, recent psychoacoustic work in the laboratory have demonstrated unusually acute temporal resolving power in birds, especially the zebra finch (e.g. Dooling et al. 2002; Dooling and Lohr 2006), which would be important in the perception of reverberated sounds.

The proposed study will involve three well-known domesticated bird species that have been widely used in controlled psychophysical experiments investigating bird hearing. The focus will be on two songbird species (oscines), the canary and the zebra finch, and the budgerigar as an example of a non-oscine bird (see below). Despite their domestication, it is known from extensive comparative studies that their auditory sensitivity corresponds well to that of their wild counterpart and of other wild passerines and non-passerines, including hummingbirds and screech owls (e.g. Farabaugh and Dooling 1996; Farabaugh 1998; Brittan-Powell and Dooling 2004; Brittan-Powell et al. 2005). In addition, their frequency region of best

hearing falls within the frequency range of the peak power of their most common vocalizations. The choice of domesticated birds was steered by previous experimental experience with these animals, which has shown their tractability in the lab and their suitability as models for investigations of the auditory system of small song and non-song birds.

2.2.2 The Budgerigar *Melopsittacus undulatus*

The budgerigar is a small, strongly social flock-living parrot species and can be found throughout a range of semi-arid and sub-humid parts of Australia. It is highly nomadic, usually moving to areas that have experienced recent precipitation, and thus likely experience changes in vegetation type and density. Both sexes produce a wide variety of learned vocalizations, most of which are used in short range communication among the large number of flock members (up to several thousand) to coordinate breeding efforts and other social behaviors. The precise function of the various call types is still unknown, but it is suggested that they have an important role in locating, recognizing, and maintaining contact with mates and flock members. The most prominent vocalization heard in a flock is the highly melodic warble song that is characterized as a continuous, very variable sequence of large numbers of song elements and syllables. This sequence often lasts up to several minutes and is mainly produced by males during courtship but can also be heard when females are absent. Warble song is thought to serve bond formation and maintenance between flock mates in general and between males and females in particular. Many of the calls and song elements of typical budgerigar

vocalizations are tonal, whistle-like sounds that can be considerably frequency-modulated. (Farabaugh et al. 1994; Farabaugh and Dooling 1996; Farabaugh 1998)

2.2.3 The Zebra Finch *Taeniopygia guttata*

The zebra finch is the most common estrildid finch of Central Australia. They prefer savanna and subtropical dry habitats without vegetation or areas with scattered shrubs and small trees. They live in colonies, which contain 50-100 individuals, and they often travel over large distances to find food. They sing alone or in groups and are able to recognize group members by their songs which allows them to chase away strangers. Females do not sing, but males use their loud and truly unique song to attract mates and, in some cases, to defend territory-like areas around the nesting site. Zebra finches are thus able to communicate over short as well as moderate distances. Males incorporate sounds of their relatives and their surroundings into their songs and they produce a hissing sound when protecting their territory and mates. Calls and song syllables are broadband, strongly harmonic sounds that can contain some, albeit little, frequency modulation. (Cynx et al. 1990; Cynx and Nottebohm 1992; Jones et al. 1996; Zann 1996; Vriends 1997; Roper and Zann 2006)

2.2.4 The Canary *Serinus canarius*

Canaries are, like the zebra finches, passerine birds. They belong to the genus *Serinus* of the finch family *Fringillidae*. Canaries are native to the Azores, the Canary Islands, and Madeira. Wild birds can be found in a wide range of habitats, including

forests and sand dunes, but inhabit most commonly semi-open habitats, such as orchards. Although they are territorial animals, they often form flocks when feeding. Their song, which is mainly used during the mating season, serves in territory defense and mate attraction and can be heard over short and long distances. It can have a large variety of syllable types and is characterized by its often several seconds long trills. Overall, their sounds are rather tonal in character and much less frequency modulated. Songs and calls also hardly have any harmonic structure compared to zebra finch calls, and canaries are known to have relatively poor frequency resolution compared to the other two species. (Hinde and Steel 1976; Nottebohm and Nottebohm 1978; Nottebohm 1981; Nottebohm et al. 1986; Dooling et al. 1992)

2.2.5 Measuring Auditory Sensitivities in the Lab

In contrast to experiments with animals in the field, operant conditioning paradigms in the lab enable the researcher to control and manipulate the test subjects' motivation to respond in a variety of psychophysical tasks. The rationale for the different experimental designs, which will be explained in detail later (Chapter 3), and the employed response measure are based on Signal Detection Theory (see e.g. Green and Swets 1966). According to this theory, a standardized sensitivity index (or discrimination measure) *d'* can be derived, which allows for valid performance comparisons across studies, species and experimental conditions. It represents the perceived difference between two stimuli or stimulus conditions. When a test subject correctly reports the presence of a stimulus

(detection) or the presence of a particular stimulus compared to a standard (discrimination), the response will be recorded as a "hit", whereas a response to an absent stimulus or the wrong one would be scored as a "false alarm". Obviously, hit rates alone are not entirely conclusive if false alarm rates are high or vary greatly. For example, an individual may score a hit rate of 75% and a false alarm rate of 60%. Although the individual had a hit rate above chance, the false alarm rate is too high to conclude that the subject in fact is able to reliably detect or discriminate the tested stimuli. In cases where false alarm rates vary or rise above about 20%, it thus has become general practice to convert all hit and false alarm rates to the sensitivity index d', which is based on relative z-scores for both hit and false alarm rates, i.e. standard deviation units of the normal distribution:

$$d' = z\,(\text{hit rate}) - z\,(\text{false alarm rate})^{*}$$

The index accounts for the discrepancy between the two measures (hit and false alarm) and thus controls for individually different response proclivities (Green and Swets 1966). 4.65 is the largest possible finite value of d' and corresponds to an essentially perfect performance with a hit rate of ≥ 0.99 and false alarm rates of ≤ 0.01 (Macmillan and Creelman 1991, 2005). In contrast, a d' equal or close to 0 implies that the subject's performance is not under stimulus control and that even high hit rates are not dependent on the presented stimuli and thus do not adequately reflect a subject's perceptual ability. In the example above with a 75% hit rate and 60% false alarm rate, the test subject's perceptual sensitivity is equal to

[*] All computational steps involved in the conversions to d' are listed in Appendix I and can also be found in Macmillan & Creelman (1991, 2005).

a d' of 0.42, whereas the same hit rate yields the much higher d' of 2.32, if the false alarm rate is only 5%. Moderate performance in terms of d' is considered to be in the neighborhood of 1.0 and 2.0. For example, correct responses on 75% or 69% of all trials (i.e. 75% hits and 25% false alarms, or 69% hits and 31% false alarms) yield a d' of 1.35 and 1.0, respectively. Traditionally, many researchers have used d' to define a threshold level at which the state of a certain tested feature (say, signal amplitude) results in a hit rate of 50%. As a consequence, certain d' values have become associated with performance at or around some perceptual threshold. Most commonly used values in this context are 1.0, 1.8 and 2.0 (Klump 1996, Gescheider 1985, Dooling and Okanoya 1995), with higher values being more conservative measures of sensitivity. A judgment as to which value is the most appropriate in a particular study is usually based on the perceptual task and its complexity. Alternatively, if false alarm rates are consistently low (i.e. below 20%), it is also customary to use a hit rate of about 50% as threshold. In this dissertation I use d' merely to facilitate unambiguous performance comparisons across species and experimental conditions when response proclivities varied rather than determining a sensitivity threshold. However, in order to relate d' values that were obtained for different conditions in a meaningful way, I nonetheless pre-determined specific minimum sensitivities expressed as d' at which performance levels are moderate, i.e. between 1.0 and 2.0.

Below is a list of combined hit and false alarm percentages that result in a d' of about 2.0, 1.0, and 0.5 (Table 1). This list can be referred to again in subsequent chapters.

Table 1. Hit and false alarm rates converted to d' of 2.0. 1.0, and 0.5.

d' = 2.0		**d' = 1.0**		**d' = 0.5**	
Hits	**FA**	**Hits**	**FA**	**Hits**	**FA**
90	23	90	61	90	78
80	12	80	43	80	63
70	7	70	31	70	51
60	4	60	23	60	40
50	2	50	16	50	31
40	1	40	10	40	22

Reporting d' instead of hits and false alarms is not always preferable, though. As mentioned earlier, d' accounts for differences in receiver response behaviors to enable comparisons across test subjects, conditions, species, and studies, especially when false alarm rates vary. While this is important, differences in response propensity, particularly those occurring over the course of an experiment, may be able to tell another, yet equally important story. For example, as previously described, similar d' can be obtained for high and low hit rates depending on the false alarm rate. In tasks where one or multiple stimuli have to be distinguished from one or multiple other stimuli, there are instances when comparisons of the

combination of hit and false alarm rate across experimental conditions can be useful as long as the within-individual performance and the performance within a particular condition is stable. This is because an increasingly difficult perceptual task could be reflected by four different types of performance change: (a) hit rate stays the same and false alarm increases, (b) hit rate decreases and false alarm remains constant, (c) both hit and false alarm rate decrease but hit rate decreases more, and (d) hit rate decreases, false alarm rate increases. Depending on the research questions at hand, disseminating changes in hit and false alarm rates therefore may provide important information about the relative salience or detectability of the discriminated stimuli that otherwise would get lost in a standardized measure like d'.

The psychophysical paradigms applied in the present studies always result in performances that are a combination of the birds' perceptual sensitivity and their response proclivity (e.g. Dooling and Okanoya 1995). It should therefore be noted that it is nearly impossible to fully control for an animal's response bias. A commonly used *combined* measure, which I also employed in my studies, is to control for this bias not only by calculating d' but also by ensuring that false alarm rates are consistently low (e.g. between 5 and 10%) across all test sessions, conditions, and individuals, unless varying false alarm rates across conditions is a valuable result that offers a different insight into the perceptual capabilities of the animal (see above). Therefore, to maintain consistency and gain reasonable control of response proclivity, it is customary to discard test sessions that do not fulfill the

pre-determined performance criteria. In the methods section of each study I state both the criteria I chose to determine which test sessions were included in the dataset, and the performance level expressed as d' I used against which performances across different conditions and species were compared.

3 STUDIES I-IV

3.1 Study I

Auditory Sensitivity towards Differences in Reverberation – Assessing the Usefulness of Sound Structural Changes as Distance and Environmental Cue

3.1.1 INTRODUCTION

Long–range acoustic communication in animals is central to many social interactions and has long served as a model for elucidating some important evolutionary processes that have shaped vocally-mediated exchanges among animals. Long-range signals serve vital purposes such as settling disputes among rivals and attracting future mates. All vocal exchanges, however, are faced with the challenge of getting the message across in a complex, sound-degrading environment. Sound degradation occurs when a sound signal is transmitted from a signaler to a receiver via a transmission channel. The acoustic channel of communication is the habitat or environment in which communication takes place. The effects of habitat-induced sound degradation on the acoustic signal constitute changes both in the signal's intensity (attenuation) and in its structure (distortion) (e.g. Morton 1975, Wiley and Richards 1978, 1980). Both attenuation and distortion may affect detection thresholds and interfere with discrimination and individual recognition that are based on subtle fine structural features of the vocalization (Naguib 1998; Lohr et al. 2003; Langemann and Klump 2005). While limiting vocal exchanges over long distances, SD also mediates short-range communication, in

which the interactants remain 'anonymous' to other individuals in the network, because it can make signals less conspicuous. Thus, it likely reduces the ability of eavesdroppers (unintended receivers) to intercept the vocal exchange of conspecifics, and it decreases the risk of being detected by predators. SD can thus be said to promote short-range communication among individuals of a network, such as between mates or parents and offspring (Dabelsteen et al. 1993; Dabelsteen 2005), and to potentially benefit the animal. In addition, especially birds and frogs have shown to take advantage of degradation when estimating the distance of a signaler by evaluating degradation-induced signal alterations that differ with communication distance (McGregor and Krebs 1984; Morton 1986; Shy and Morton 1986; Wilczynski and Brenowitz 1988; Brenowitz 1989; McGregor 1994; Naguib 1995, 1996b, a; Fotheringham et al. 1997; Mathevon and Aubin 1997; Naguib 1997; Holland et al. 1998; Morton 1998; Naguib 1998; Nelson 2000; Holland et al. 2001a; Naguib and Wiley 2001a). For a receiver, being able to properly range the source of a signal is often crucial in evaluating the immediate importance or urgency of a signal and in making decisions about appropriate ensuing behavior. Altogether, it is obvious that habitat-induced sound degradation both negatively and positively affects the exchange of social information (e.g. Michelsen and Larsen 1983), and selection should favor signals that effectively transmit information despite degradation (Wiley and Richards 1978, 1982; McGregor 1994; Klump 1996b), while incorporating features that degrade predictably over distance (Naguib and Wiley 2001b).

The major types of signal alterations caused by degradation are overall attenuation, frequency-dependent attenuation, reverberations, and amplitude fluctuations (e.g. Marten and Marler 1977; Michelsen 1978; Wiley and Richards 1978; Richards and Wiley 1980). Studies with humans, for instance, have shown that they can use overall amplitude changes, frequency-dependent attenuation, and reverberation as distance cues, and that distance estimation is possible even when these cues are processed separately (von Békésy 1938; Coleman 1962, 1968; Mershon and King 1975; Mershon and Bowers 1979; Mershon et al. 1989; Little et al. 1992). In fact, reverberation has shown to serve both as an absolute and a relative cue to distance (von Békésy 1960; Mershon and King 1975) compared to the other aforementioned types of degradation, which merely provide relative information regarding the distance of a source (von Békésy 1949; Coleman 1963; Mershon and King 1975; Little et al. 1992). Moreover, reverberations can provide cues regarding the acoustic quality of the surrounding environment and thereby provide what could be called an auditory 'image' of the surroundings. In contrast, with the exception of a few field studies there are at this point hardly any detailed animal studies that investigate the perception of these types of degradation-induced signal alterations and their potential usefulness as cues under controlled lab conditions. Therefore, in order to fully comprehend the ways in which degradation affects signal perception also in birds, the different effects need to be assessed in isolation first.

The goal of this study is to provide a controlled assessment of the perception of reverberation and sound scattering as the major contributors to the evaluation of sound source distances and the acoustic properties of the surroundings. The first part of my dissertation research therefore focuses on quantifying the perceptual sensitivity to sound alterations caused by reverberation and sound scattering in species-specific, heterospecific, and artificial sounds and compares this sensitivity among bird species. The focus is on within-signal structural changes in amplitude and frequency patterns over time. The birds' sensitivity towards a variety of artificially induced reverberations as well and natural, object-induced sound scattering were tested. The latter was taken from recordings of natural vocalizations transmitted in a sound-attenuated booth containing different objects, while the former was achieved by convolving sounds with a computer-implemented algorithm. Both will, among other things, reveal reverberation and scattering increments that are audible by the birds and their potential usefulness in the estimation of distance and the acoustic quality of the environment. My experiments are designed to reveal this potential, while future studies in the field are needed to test whether such features of reverberation and other forms of scattering indeed are used by birds, either alone or in combination with other distance, location, and environmental cues.

Because reverberation and scattering greatly affect the temporal structure of the signal, good temporal resolution should be pivotal in hearing signal alterations brought about by this type of degradation. Based on previous studies

(Dooling 1982, 1989, 1991; Dooling et al. 2000a; Dooling et al. 2002; Dooling 2004) birds should have adequate temporal resolving power to assess such reverberation- and scattering-induced differences. I therefore expect that all three tested species are able to hear small structural signal changes that are brought about even by low levels of reverberation and scattering. This ability is likely higher for sounds with broad frequency spectra and high amplitude modulation (AM) than for tonal sounds with a narrow spectral band or rapid linear frequency changes and low AM. I further hypothesize that changes in the temporal envelope alone can be used by birds to assess the presence of reverberation and that these could offer useful distance cues and could help in evaluating the environment via its acoustic quality.

If there are species-specific auditory system adaptations, all three species should perform better with their own vocalizations than with those of other species. Consequently, one could assume that a bird also performs better when any other test stimulus is at a frequency typical for its own vocalizations or is equal to the species' frequency of best hearing and highest temporal and frequency resolution. Findings like these could reveal potential species adaptations to the predominant type of vocalizations used in intraspecific communication, which in turn may be an adaptation to the species-typical acoustic environment. This study is designed to provide a first insight into the potential of within-signal changes brought about by reverberation and scattering to serve as possible distance and environmental cue in addition to level differences and echoes that accumulate over distance.

3.1.2 METHODS

Subjects

The test subjects in this experiment were four budgerigars (2 males, 2 females; *Melopsittacus undulatus*), four canaries (males only; *Serinus canarius*), and four zebra finches (2 males, 2 females; *Taeniopygia guttata*). Zebra finches were offspring from birds obtained from commercial dealers and raised in our vivarium, while budgies and canaries were first generation birds from dealers. Hearing abilities of all birds were tested prior to choosing them as test subjects (see below), and only birds with normal, species-specific auditory tuning curves were used in experiments. Birds were housed in individual cages (approximately 30 x 30 x 20 cm) in a vivarium at the University of Maryland with ad libitum access to water and kept on a constant light-dark cycle to avoid potential season-induced changes in hearing sensitivity. Food access was individually controlled and birds were weighed daily to keep them between 85 and 90% of their free-feeding weight. The birds' daily diet comprised standard parakeet, canary and finch seed mixes. Yellow millet was used as reinforcement during experimental sessions.

All canaries were chosen to be males only, because canaries are seasonal breeders. Although females are prevented from entering breeding conditions when used in experiments by subjecting them to non-seasonal diurnal rhythms and away from interactions with males, I wanted to avoid any potential concurrent auditory system changes that nonetheless could occur and, as a consequence, affect the auditory sensitivity of females.

Experimental Apparatus[†]

Subjects were tested in a psychophysical set-up consisting of a wire cage (approx. 25 cm^3) with a response panel and food hopper mounted in a sound-isolating booth (Industrial Acoustics Company, Inc., Bronx, NY, USA). The response panel was made up of two horizontally aligned LED keys that were attached to micro-switches (for more details see Park et al. 1985; Dooling and Okanoya 1995). The microswitches were triggered as soon as the bird pecked the corresponding LED. The left (green) LED served as observation key and the right (red) LED as report key. Experimental events and sound playback were controlled by a computer and Tucker-Davis Technologies (TDT, Gainsville, FL) System III modules (filter, attenuator, amplifier, and mixer), respectively. Acoustic stimuli were played through a KEF 80C speaker (KEF Electronics, Maidstone, UK) that was mounted approximately 40 cm above the bird's head, directly facing it from the front. All sound stimuli were passed through a programmable 2-channel signal processor (TDT, RX6 module), attenuator (TDT, PA5 module), and mixer (TDT SM5 module), and were subsequently amplified by a Crown D-75 amplifier. The output sampling frequency (fs) of all stimuli was 24,414 Hz. The birds' behavior was monitored during training and experimental sessions via a Sony HVM-322 video camera system.

[*]Please note that the same experimental apparatus was used in all studies presented in this dissertation and will therefore not be fully described in subsequent studies.

Psychophysical Task – Training and Testing

Birds were shaped with operant conditioning methods to obtain a food reward by pecking response keys (LEDs) upon detecting a sound. Prior to the experiments, audiograms for all test subjects were obtained to assure that all birds had normal hearing. Subjects were subsequently trained in an Alternating Sound Task, in which they had to detect a change in a continuously repeated ('background') sound that was played back at fixed 500 ms intervals. In an Alternating Sound Task, the change to be detected is a new ('target') sound that is chosen randomly among seven targets after varying time intervals (for further details on training procedures see Park et al. 1985; Okanoya and Dooling 1988; Dooling and Okanoya 1995). For initiation of a trial the birds have to peck the left LED (green), which starts a timer with a random interval of 2-6 s, after which the next peck results in the presentation of a randomly chosen target sound. If the bird pecks the right LED (red) within 2 s after target presentation, it obtains a 1.5-s access to food (yellow millet seeds), and the response is recorded as a "hit". A failure of the bird to detect the target (i.e. a failure to discriminate it from the repeated background stimulus) is defined and scored as a "miss" and a new trial begins.

Birds were tested twice daily in sessions of 100 trials in the morning and afternoon. The 100 trials consisted of 10 blocks of 10 trials, with each block including a random presentation of the seven targets as well as three shams, in which no target was presented and the background was played back instead (33% of all trials). Responses during sham trials were recorded as either "false alarm"

(peck at response key) or “correct rejection” (no peck at response key). False alarms were punished with a 6-s blackout, during which the birds sat in the dark.

In test sessions, the non-reverberated version of a stimulus served as repeated background. The seven target sounds to be alternated with and detected in the repeated background consisted of the same sound stimulus at seven different degrees of reverberation (induced artificially or naturally, see above). Birds were tested until they showed no further improvement in performance for two successive sessions of 100 trials (i.e. high hit rate and low false alarm rate below 20%). These last 200 trials were then included in the final data set for subsequent analysis. Sessions with a false alarm rate exceeding 20% were discarded. The number of sessions it took to reach the point of no improvement and show consistent performance with low false alarm rates for 200 consecutive trials varied depending on the degree of difficulty of the perceptual task.

Birds were also tested in control experiments, in which some of the target stimuli were the same as the alternating, non-reverberated background sound (with a reverb time of 0ms). This was to test for any potential acoustic differences arising from the mere playback of background vs. target stimuli and their potential use in discrimination.

Data Collection

Data records of hit and false alarm rates were converted to the sensitivity index d’, which ensures unbiased comparisons of hearing sensitivities toward signal alterations across conditions and species (Gescheider 1985; Dooling and Okanoya

1995; Klump 1996b; see also 2.2.5 "Measuring Auditory Sensitivities in the Lab"). Additionally, in order to evaluate differences in d' between conditions in a meaningful way, Bonferroni-adjusted 95% confidence interval around the mean d' value of each condition were constructed. If intervals did not overlap, the performance or response sensitivity (d') in these conditions was significantly different (Macmillan and Creelman 2005). Depending on the difficulty of the perceptual task, performances were compared against a moderate sensitivity value of 1.0 or 2.0, which correspond to hit and false alarm rates of e.g. 50% (hits) and 16% (false alarms) and 50% (hits) and 2% (false alarm), respectively. The less conservative value (1.0) was used in experiments where the tested factors had significant effects on performance but the majority of obtained sensitivities were mainly between 2.0 and 1.0. This allowed me to track obtained sensitivities against a set minimum performance level without obliterating potentially interesting results.

Stimuli & Sound Degradation[**]

EXPERIMENT 1 – ARTIFICIAL REVERBERATION:

All subjects were tested with artificial sound stimuli and segments of natural vocalization that all were between 200 and 250 ms in duration. This duration limit was chosen to avoid any perceptual advantage or disadvantage brought about by significantly longer or shorter durations of some sounds while at the same time

[**] The procedure for artificial reverberation of stimuli is the same throughout this thesis and will therefore not be repeated in detail in subsequent studies.

allowing for approximately equal benefits gained by temporal integration, which typically occurs up to approximately 100-300 ms for humans (Plomp and Bouman 1959; Zwislocki 1960; Watson and Gengel 1969) and 200-250 ms for birds (Dooling 1979; Dooling and Searcy 1985; Klump and Maier 1990; Okanoya and Dooling 1990). The following is a list of all test stimuli:

1. Artificial stimuli (Examples see Figure 1)
   (a) three different pure tones of 1, 2, and 4 kHz
   (b) tonal upsweep from 1-4 kHz that covers the frequency range of best hearing in all three species
   (c) band-limited white noise band-pass filtered at 0.5 – 8 kHz that covers the typical hearing range of these species

Stimuli (a), (b), and (c) were all digitized using SigPro 3.23 (Simon B. Pedersen, Center for Sound Communication, Universities of Copenhagen and Southern Denmark). Stimuli like these have been successfully used in the past to test basic hearing capabilities. The choice of these stimuli allows for data obtained in this experiment to complement previous results.

2. Natural stimuli (Examples see Figure 1)
   (a) a common budgerigar contact call (tonal and broadband, with rapid FM)
   (b) a common canary song syllable (narrow spectrum, tonal, *with* second harmonic)
   (c) the same canary syllable *without* second harmonic

(d) a common zebra finch song syllable (broadband, with rapid AM and high harmonic content)

All natural stimuli were selected from our lab's library of recordings that were made from individuals that had died at least 2 years prior to this study. Vocalizations had been recorded with a Marantz PMD670 digital recorder and an Audio-Technica Pro 35ax directional microphone at a sampling frequency of 48,000 Hz (16 bit) and in a sound attenuating chamber at a distance of no more than 1 m from the bird. I selected only high quality, noise-free recordings that were representative vocalizations of the respective species and the individual.

3. Natural stimuli with noise masker

The noise masker was a 2-min loop of random white noise that was generated in Matlab 7.5.0 (R2007b, The Mathworks Inc. 2007) and played back as the continuous background noise at a constant level. The noise was band-passed between 0.5 and 8 kHz and attenuated to two different spectrum levels (per cycle energy distribution, i.e. dB/Hz)[‡] of 21.3 and 31.3 dB that corresponded to an overall noise level of 60 and 70 dB SPL (A). In tests with background noise, the level of the sounds to be discriminated in noise was not roved by ±3 dB. Only the natural vocalization segments listed above were used in noise experiments, and the birds were tested exclusively with their species' own vocalization.

[‡] Spectrum level is calculated by first converting the measured noise SPL into pressure P (in Pa): $20\ log\ P\ = noise\ SPL$ (solve for P). Spectrum level is then equal to 10 log $\frac{P^2}{bandwidth}$, with bandwidth = width of noise band.

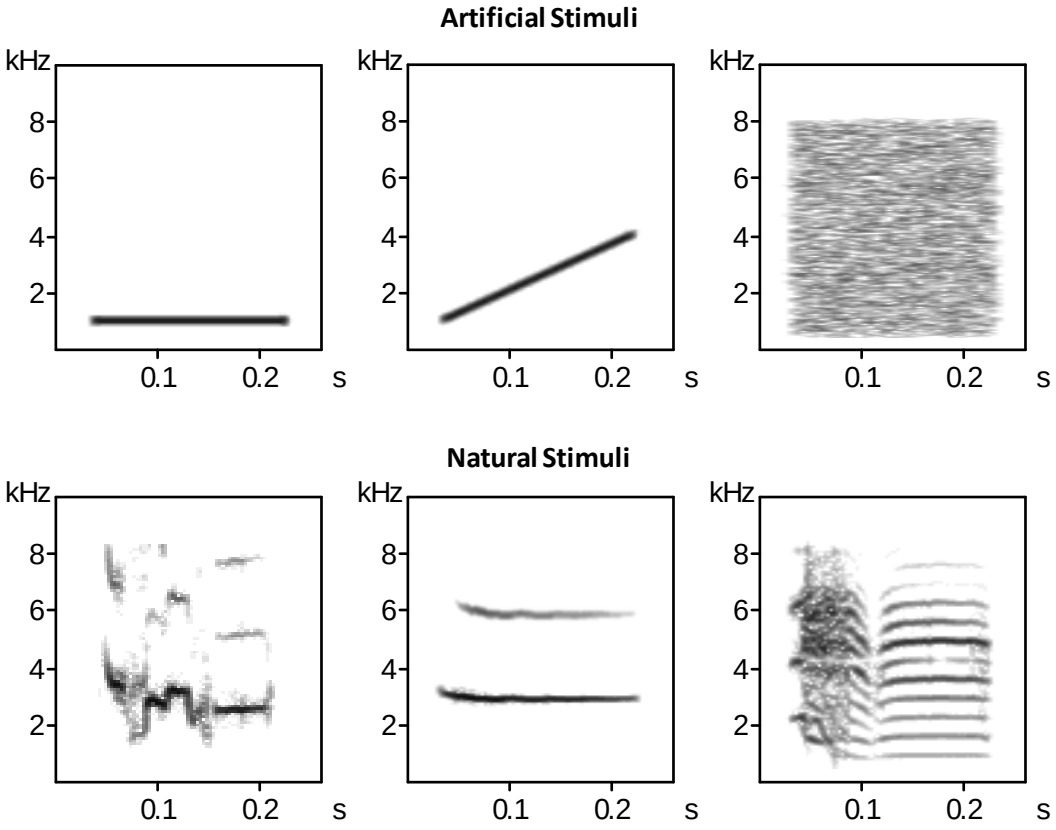


Figure 1. Six examples of artificial and natural stimuli used in Experiment 1. Spectrograms of artificial stimuli, left to right: 1 kHz pure tone, 1-4 kHz tonal upsweep, band-limited white noise. Spectrograms of Natural stimuli, left to right: budgerigar contact call, canary song syllable, zebra finch song syllable. Frequency (in kHz) is on the y- and time (in s) on the x-axis.

Reverberation of Artificial and Natural Stimuli

Reverberation times are frequently measured as the decay rate of the signal energy upon termination of an impulse (e.g. Waser and Brown 1986; Mershon et al. 1989; Holland et al. 2001a) or as the ratio of the integrated echo and signal energy (Richards and Wiley 1980; Dabelsteen et al. 1993; Holland et al. 1998; Balsby et al. 2003; Blumenrath and Dabelsteen 2004; Blumenrath et al. 2004; Lampe et al. 2007)

as well as the length of the echoes' energy quartiles (Blumenrath and Dabelsteen 2004). Here, test stimuli were artificially reverberated using a FFT-based computational model in Matlab 7.5.0. The computer-implemented algorithm involved an exponentially decaying impulse response using Gaussian noise (programming code in Appendix II). This algorithm requires the specification of a reverberation time, which is defined as the time it takes for the sound energy to decay 60 dB after sound offset (i.e. after the sound source is 'turned off'). It will in the following also be referred to as "reverberation time" or a its abbreviation "RT(60)." Twenty-one reverberation times were used to compare against the non-reverberated stimulus, ranging from 200 ms down to as little as 1 ms. Times were decreased in two increments of 50 ms (200, 150, and 100 ms), and nine increments of 10 ms (100, 90, 80, 70, 60, 50, 40, 30, 20, and 10 ms) and of 1 ms (10, 9, 8, 7, 6, 5, 4, 3, 2, and 1 ms), respectively, yielding altogether 21 reverberation times (examples are shown in Figure 2). I additionally used a reverberation time of 0 ms to create the non-degraded sound, which served as background or comparison stimulus. Although this may seem redundant, subjecting all stimuli to the same signal processing procedures ensured that any detected difference in the fine structural details of the sound were due to the specified reverberation times alone and not also to the type and amount of signal processing the sounds were subjected to.

The algorithm I used is a simplified model of reverberation as it occurs in many environments. My decision to employ this simplified model was motivated by

a wish to find an approach that is easily replicable and can be generalized across habitat types. Previous studies found that the precise reverberation pattern as measured by the blur ratio, tail-to-signal-ratio, and the energy quartiles of the echoes is highly variable with season, within the same habitat and more so across habitats, even if the same methodology and equipment is employed (Nemeth et al. 2001; Balsby et al. 2003; Blumenrath and Dabelsteen 2004; Lampe et al. 2007; Barker et al. 2009).

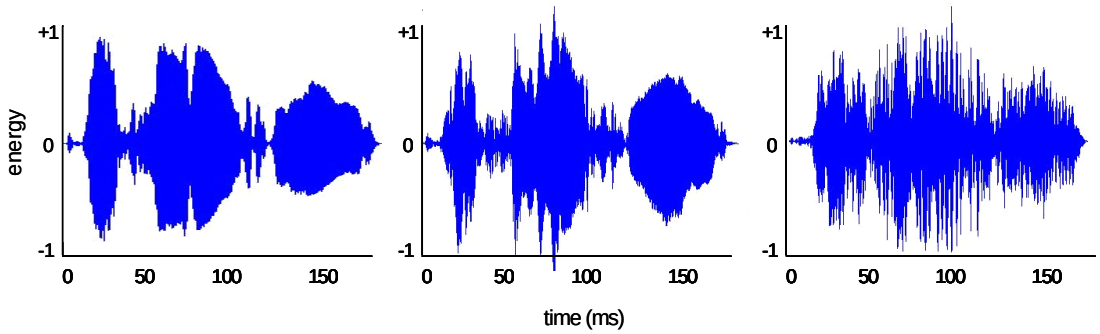


Figure 2. Time waveform (oscillogram) of three artificially degraded versions of the same budgerigar call, which were used as stimuli. Left: not reverberated (0 ms); middle: RT(60) = 1 ms; right: RT(60) = 100 ms. Note that all resulting echo tails were removed.

Psychophysical Tests

The 21 reverberation times of each stimulus served as targets that had to be compared to the repeated, non-reverberated background stimulus (0 ms reverberation time). Birds had to be tested in three different sets of sessions per stimulus type to complete experiments with all 21 targets. (See "Psychophysical Task – Training and Testing" and "Data Collection" above for more details.)

EXPERIMENT 2 – NATURAL SCATTERING:

Only the natural vocalizations listed above were used in this experiment (budgerigar call, canary syllable with harmonic, zebra finch syllable).

Scattering of Stimuli

For naturally induced scattering, sounds were transmitted from a JBL Pro III loudspeaker in an anechoic chamber (H x W x D: 2.10 x 2.74 x 2.54 m) and re-recorded at a sampling frequency of 48,000 Hz with a Audio-Technica Pro 35ax directional microphone situated at a distance of 2.45 m from the speaker. Objects were placed in the direct transmission path exactly half-way between speaker and microphone, and recordings were made without and with the presence of the following objects:

(a) a rectangular cardboard box (H x W x D: 0.46 x 0.30 x 0.19 m) filled with Styrofoam beans

(b) approximately 2 m tall and 1.5 m wide holly (*Ilex aquifolium*) branches

The presence of the box was varied by three different positions relative to the transmission pathway (at 0°, 45°, 90°), whereas branch presence was only varied in number (one vs. two branches). Appendix IV illustrates the positions of the box and shows pictures of the holly branch set-up.

The transmission sequences consisted of five stimulus sequences, each with different order of stimuli, and the sounds in each sequence were separated by 1s of silence. Sounds were played back from a Dell Latitude E6400 laptop computer using SigPro 3.23 (Simon B. Pedersen, see above) and amplified with a Crown D-75

amplifier to a constant SPL of 90 dB (A, source level), which corresponds to the average natural sound intensity of most bird song at its source. Sound intensity was measured with a Larson & Davies System 824 sound pressure level meter (A-filter, fast setting) equipped with a Larsen & Davies ½" omnidirectional condenser microphone (model 2540). Transmitted sequences were recorded digitally with a Marantz PMD670 digital recorder at a sampling frequency of 48,000 Hz (16 bit) and constant input level. Recordings were made separately for each condition, yielding a total of 6 recordings (no object; box at 0°, 45°, and 90°; 1 and 2 tree branches). I band-pass filtered all recorded vocalizations with sound-specific filter settings. Further signal processing procedures are described in detail below ("Signal Processing and Sound Playback").

Psychophysical Tests:

Recordings that were made without the presence of any objects were used to obtain the non-reverberated stimuli that served as a background or comparison stimulus in subsequent experiments with birds. All other stimuli served both as target and background stimuli. The following is a list of all background-target combinations that the birds were tested with:

- Repeated background: no object – Targets: box at 0°, 45°, and 90°
- Repeated background: box at 0° – Targets: no box, box at 45° and 90°
- Repeated background: box at 45° – Targets: no box, box at 0° and 90°
- Repeated background: no object – Targets: 1 tree branch, 2 tree branches

- Repeated background: 1 tree branch – Targets: no tree branch, 2 tree branches
- Repeated background: 2 tree branches – Targets: no tree branch, 1 tree branches

EXPERIMENT 3 – STRUCTURALLY DECOMPOSED STIMULI

The acoustic stimuli used in this experiment were added post-hoc to test for the relative importance of temporal and spectral patterns in the discrimination of reverberation differences and the fine structural details that constitute the quality or potential timbre of the sound. The latter is eliminated by for instance substituting the natural stimulus with non-random white noise, while conserving the amplitude envelope of the original vocalization. This was a preliminary experiment with the sole intention to gain a first insight into the role of changes in the sounds' fine structural details in the discrimination of reverberation times. All non-reverberated and reverberated versions of some of the natural stimuli from Experiment 1 were used as basis for the decomposition to test whether reverberation-induced changes in the overall amplitude function of the sounds was important for correct discrimination. I created non-random (i.e. same seed) white noise stimuli in Matlab 7.5.0 and imposed on them the envelope function of the reverberated and non-reverberated budgerigar call and zebra finch syllable. The envelope function was extracted for the entire spectrum of each sound by using Hilbert transformation. I used noise that was generated with the same seed (pseudo-random number generator) to make sure that the fine structure of the

noise used in each case was the same and could not serve as a cue. In preliminary experiments with stimuli made up of random noise, the birds were somewhat able to discriminate between noise segments generated with different seeds based on the resulting fine structural details alone. The frequency range of these noise-substituted signals was equal to the range of the original vocalizations. The precise algorithms for these procedures can be found in Appendix III.

Psychophysical Tests

The 21 reverberation times of each stimulus from Experiment 1 above served as targets that had to be compared to the repeated, non-reverberated background stimulus (0 ms reverberation time). Birds had to be tested in three different sets of sessions per stimulus type to complete experiments with all 21 targets. (See "Psychophysical Task – Training and Testing" and "Data Collection" above for more details.)

Signal Processing and Sound Playback

In order to test for the impact of reverberations on the distinctive structural features within the original time frame of the sounds, all reverberated signals were additionally signal-processed to remove tails of echoes, leaving only distortions within the signal as potential difference cues. I applied a ½ Hann window with a size of 10 ms as tapering function to the cut ends in Matlab 7.5.0. This function is preferable to the frequently used cosine taper function as it is more effective in reducing spectral spread, if short rise and fall times are used.

After digitally normalizing all test signals to the same peak RMS value and applying sound-specific band-pass filters to remove potentially amplified background noise, they were additionally adjusted to an equal peak SPL of 60 and 70 dB (A, fast setting; supra-threshold level) for experiments with and without simultaneous noise masker, respectively. This is a comfortable listening level for birds and equivalent to a bird singing at a distance of about 10-30 m (typical source level (at 1 m): 90 dB). To avoid any remaining level differences serving as discrimination cues, the level at which the test sounds were played were additionally roved randomly by a maximum of ± 3 dB, except in experiments with masking noise. Sound pressure levels were measured using a Larson-Davis System 824 sound level meter, which uses a detector with a 125 ms time constant (fast setting).

Statistics

Results obtained for artificial reverberation, natural reverberation and noise maskers (Experiments 1 and 2) were analyzed separately with a within-subject (or repeated measures) Analysis of Variance to determine the main effect of reverberation time, stimulus type, object presence and position, and background noise on the subject's performance as well as their interaction. Species served as the independent, between-subjects factor which divided all subjects into groups. (For details on repeated measures ANOVA designs with one between-subjects factor refer to Hand and Taylor 1987, p. 125.). Results for the artificially reverberated artificial and natural stimuli were also analyzed separately. The data

distribution for each of these experiments was tested for normality, variance homogeneity (Levene's Test) and sphericity (Mauchley's Test) prior to applying the aforementioned tests. I additionally inspected Spread-versus-Level Plots that graph standard deviations against factor level means. If sphericity was violated for some factors, but assumptions of normality and variance homogeneity were otherwise fulfilled, Greenhouse-Geisser adjustments were used to decrease the probability of committing a Type 1 error. This adjustment applies a correction factor to the degrees of freedom (*df*) of the *F*-distribution. Repeated Measures ANOVAs were followed by Bonferroni-adjusted post-hoc pairwise multiple comparisons (using 95% confidence intervals) to identify specific significant differences between factor levels. This is a generally accepted procedure from a Signal Detection Theory viewpoint (Macmillan and Creelman 2005) and corresponds well with recommended statistical analyses for Repeated Measures ANOVAs.

Experiment 3 with structurally decomposed stimuli provided data whose distribution called for non-parametric tests. The results obtained in Experiment 3 with non-random noise (with imposed amplitude envelope of natural sounds) were analyzed using a Wilcoxon Signed-Rank Test for two related samples. The purpose here was to compare the performance of birds with the envelope-imposed noise stimuli and the original natural stimuli, which provided the amplitude envelope function imposed on the noise. All tests were conducted using SPSS (PASW Statistics 18, 2009).

3.1.3 RESULTS AND DISCUSSION

Initial control experiments with the non-degraded stimulus serving as both background and target stimulus did not show any perceptual differentiation based purely on acoustic differences in playback in any of the experiments described below.

EXPERIMENT 1 – ARTIFICIAL REVERBERATION:

1. Artificial stimuli

All three main factors (species (SP), sound type (ST), and reverberation time (RT)) had strongly significant effects on the birds' ability to discriminate between non-reverberated and reverberated stimuli (Table 1), with sound type and species explaining most of the data variation (ST: $\eta^2 = 0.969$; SP: $\eta^2 = 0.908$ vs. RT: $\eta^2 = 0.863$)[§]. Post hoc multiple comparisons using Bonferroni adjusted 95% CIs revealed that on average canaries showed a significantly lower perceptual sensitivity (as indicated by the smaller mean value for d') than either of the other two species (Figure 3 (a)). It was, in fact, just below the set value of d' = 2.0, which indicates a moderate performance level (e.g. 50% hits, 2% false alarms). Budgerigars, on the

[§] Classical and partial eta-square (η^2) values are measures of strength of association frequently reported in multifactor ANOVA designs. Both are descriptive indices of association strength between a main or interaction effect and a dependent variable. An important and often neglected distinction is that classical η^2 is defined as the proportion of total variation attributable to the factor and thus ranges from 0 to 1 (classical $\eta^2 = SS_{factor}/SS_{total}$, SS_{factor} = variation attributed to the factor, SS_{total} = total variation in the dataset). Partial η^2 also ranges from 0 to 1 and denotes the proportion of total variation caused by the factor, but it is calculated as $SS_{factor}/(SS_{factor} + SS_{error})$. Since in a multifactor ANOVA $SS_{factor} + SS_{error}$ is usually less than SS_{total}, reported partial η^2 values are typically greater than classical η^2 values, and the sum of all partial η^2 is often greater than 1. SPSS only provides partial η^2, which I here employ merely as a relative measure of association strength. ***Pierce, C. A., Block, R. A. & Aguinis, H.*** *2004. Cautionary note on reporting eta-squared values from multifactor ANOVA designs. Educational and Psychological Measurement, 64, 916.*

other hand, performed best on average but not significantly better than zebra finches. When comparing pooled data for different reverberation times (Figure 3 (c)), sensitivity decreased considerably and moderate levels of performance were generally reached at a reverberation time of 3 ms. There was, however, a significant interaction effect between reverberation time and signal type (Table 1), and Figure 4 (c) clearly shows that discrimination abilities greatly varied between stimuli. For instance, the birds' sensitivity toward reverberation differences for white noise stimuli was consistently well above d' = 2.0 for all reverberation times, whereas the birds' performance was mostly below this value when presented with pure tone stimuli of 1 and 2 kHz. Again, differences among the three species were also apparent. The canary's discrimination sensitivity decreased to a d' of 2.0 at high

Table 1. Repeated Measures ANOVA table showing univariate results for between- and within-subjects effects and their interactions ($\alpha = 0.05$). The model uses Type IV Sums of Squares for balanced designs. *Greenhouse-Geisser adjustment of values where sphericity could not be assumed. Strongest significant effects on performance are (in descending order): sound type, reverberation time, species, and the interaction between sound type x reverberation time.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Between-Subjects*					
Species	2	122.104	61.052	19.686	0.009
(2) *Within-Subjects*					
Sound Type	3	899.419	299.806	123.529	<0.001
Reverberation Time	20	156.115	7.805	25.197	<0.001
(2) *Interactions*					
Species x Sound Type	6	31.973	5.329	2.196	0.116
Species x Reverberation Time	*6.257	22.144	*3.539	1.787	*0.180
Sound Type x Reverberation Time	*3.696	165.168	*44.689	9.708	*0.001

reverberation times, whereas budgerigars reached this performance level at low levels (Figure 4 (b)). Zebra finches were again closer to budgerigars in terms of

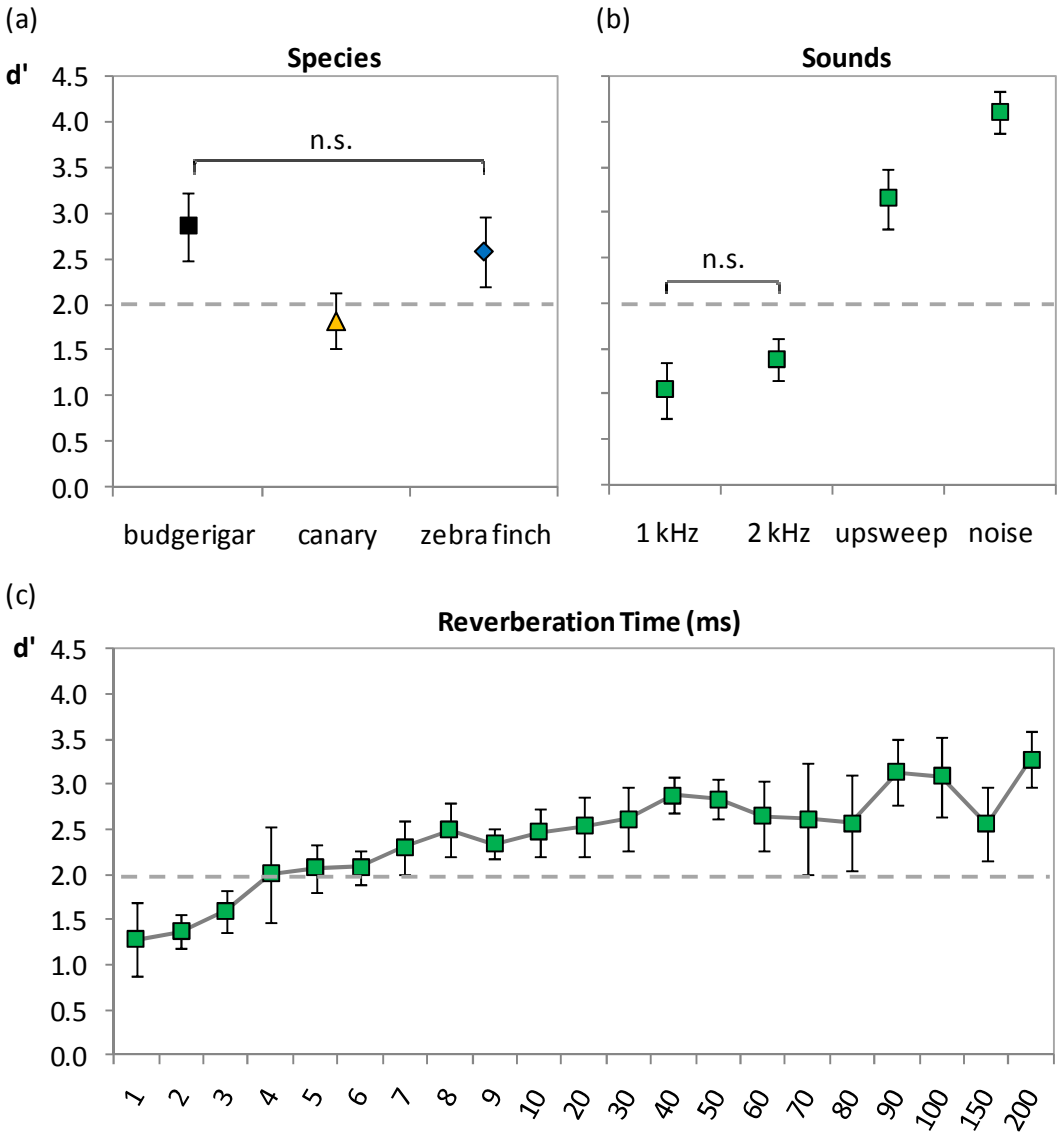


Figure 3. Significant main effects (a)-(c). Performance was greatly dependent on the tested species, stimulus type, and reverberation. Pure tones caused average performance to drop significantly compared to broader-band sounds (b), and canaries were generally less sensitive toward sound differences caused by reverberation (a). Generally, lower reverberation times were perceived less readily than higher levels (c). For factors "species" and "sounds" only non-significant differences between factor levels are marked (n.s.). Significant differences between levels of "reverberation time" exist, if the respective 95% Bonferroni-adjusted CIs do not overlap. Stippled lines represent a discrimination sensitivity of d' = 2.0 equivalent to a moderate performance level.

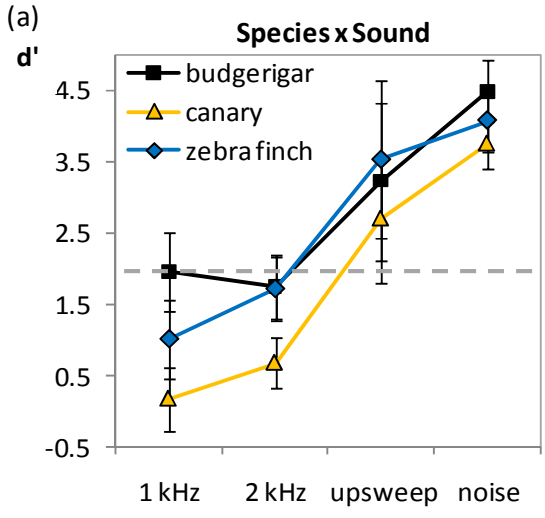
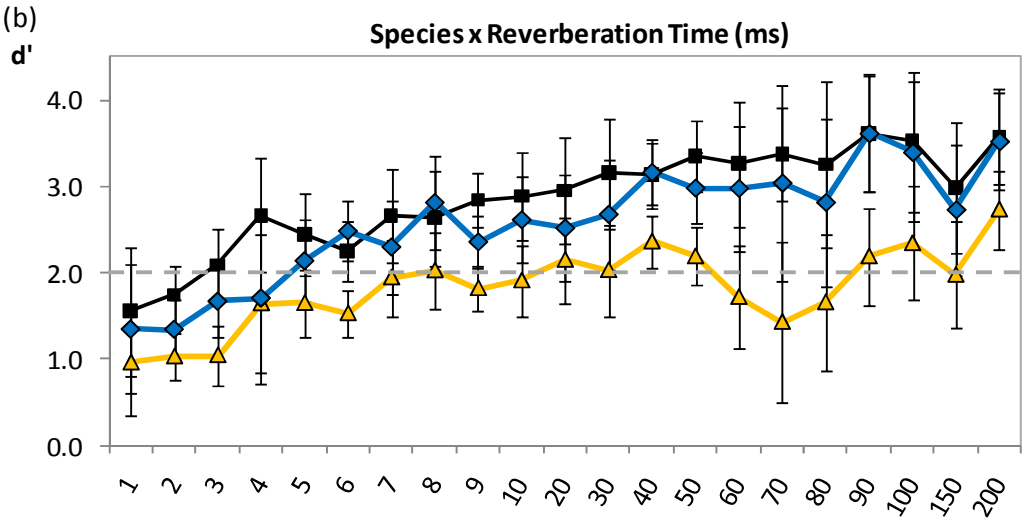
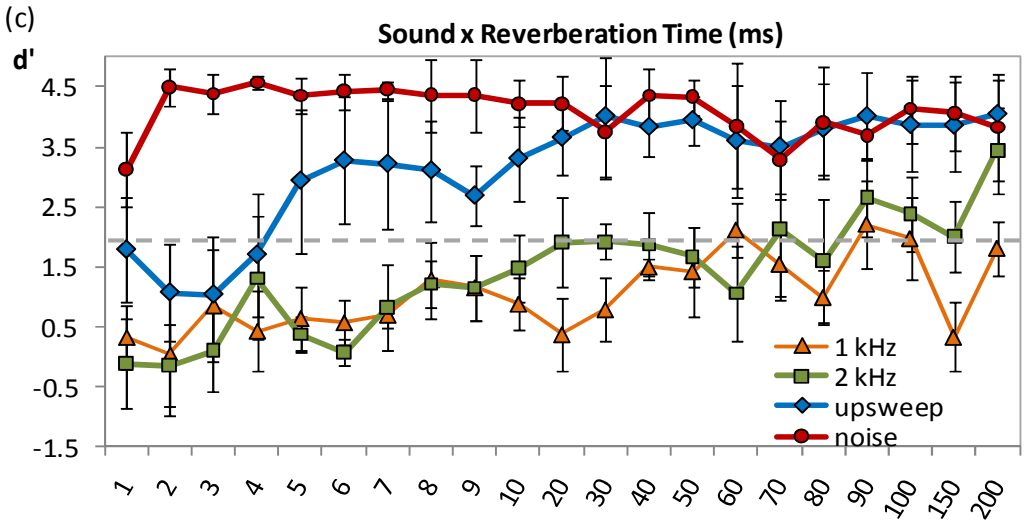


Figure 4. Interaction effects between species and sound (n.s.), species and reverberation time (n.s.), and sound and reverberation time (sign.). Performance is lowest for canaries and highest for budgerigars across all vocalizations and reverberation levels (a)+(b). Especially with pure tones, canaries were no longer under stimulus control (d' approaching 0). Performance remains rather constant for noise stimuli independent of reverberation levels (c) but gradually decreases with decreasing reverberation levels for other stimuli. Stippled lines mark a discrimination sensitivity of d' = 2.0. Bars represent Bonferroni-adjusted 95% CIs around estimated marginal means.





performance. Although canaries generally were much worse than the other two species at distinguishing between the absence and presence of specific levels of reverberation, they were nonetheless very well capable of performing this task without great difficulty if the sounds were either upsweeps or white noise, i.e. stimuli with a much broader spectrum.

It is somewhat surprising that a species with large amounts of pure-tone-like stimuli in their repertoire (canaries) should perform worse than a species with exclusively noisy, broad-spectral sounds (zebra finches) when distinguishing non-reverberated from reverberated pure tones. Due to the commonly used types of sounds, canaries should be more 'used to' or better trained at hearing subtle differences in the fine structural details of such tonal sounds. However, zebra finches are known to have greater sensitivity toward temporal differences than either canaries or budgerigars (Lohr and Dooling 1998; Dooling et al. 2002). Since changes due to reverberation occur mainly in the temporal domain, great temporal resolution of the zebra finch auditory system could therefore have aided individuals of this species in this discrimination task. Budgerigars that show slightly higher sensitivity than the zebra finches continuously incorporate new sounds into their vocal repertoire, which also include tonal stimuli with low and high frequency modulation. Being open-ended learners, it could be argued that their perceptual and cognitive flexibility as well as their familiarity with the behavior of tonal stimuli in complex acoustic environments could be the cause for their superior perceptual capabilities.

The width of the frequency spectra of the stimuli and the overall spectral patterns (i.e. energy distribution across frequencies) seem to be pivotal in determining the sensitivity of the birds toward within-signal alterations brought about by reverberation. This would explain why reverberation differences between white noise stimuli were much more easily discriminated than differences between pure tone stimuli. For the same reason, tonal upsweeps covering a wider frequency range within the birds' frequency range of best hearing also improved performance considerably by about a d' of 2.0.

Unfortunately, only zebra finches could be tested with all tonal stimuli, including the 4 kHz pure tone. In experimental sessions with 4 kHz stimuli, budgerigars and canaries would stop initiating new trials after several failed attempts. Instead, behaviors were dominated by displacement activities[**], such as fast and random pecking at both observation and response keys, climbing all over the response panel, chewing on or ripping apart part of the cage set-up, etc. Other behaviors would include preening or simply dozing in the back corner of the cage. Experimental sessions were programmed to time out after 15 min of inactivity, but in cases of more destructive behaviors, the birds were taken out before the time-out period had expired.

Results for the complete set of tonal stimuli (1, 2, and 4 kHz, and 1-4 kHz upsweep) therefore had to be analyzed separately for zebra finches alone (Table 2, Figure 5). One can see in Table 2 that the repeated measures ANOVA yielded very

[**] Displacement activities are behaviors that are frequently observed in animals in moments of indecision and are unrelated and irrelevant to the situation at hand.

similar results for main and interaction effects as above. In addition, results for 4 kHz follow similar patterns as those for the other two pure tones (largely below a d' of 2.0) and the difference between them is non-significant (Figure 5 (a), (c)). There is, however, a tendency for zebra finches to have less difficulty hearing reverberation differences in 2 kHz tones followed by 4 kHz tones. Pooled across stimuli, performance at d' = 2.0 or below is achieved for reverberation times of less than 8 ms. The results are consistent with average audiograms of zebra finches. The frequency of greatest absolute hearing sensitivity in this species is at about 2 kHz. Sensitivity gradually declines below and above but is still higher at 4 kHz than at 1 kHz. It is therefore reasonable to assume that the sensitivity toward reverberation-induced signal changes also is greatest for sounds that fall within the frequency range of beast hearing.

Table 2. Repeated Measures ANOVA table showing univariate results for between- and within-subjects effects and their interactions for zebra finches alone ($\alpha = 0.05$). The model uses Type III Sums of Squares for balanced designs. *Greenhouse-Geisser adjustment of values where sphericity could not be assumed. All factors are significant. Factor with the strongest effect on performance is sound type as seen for all birds in Table 1.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Within-Subjects*					
Sound Type	3	268.393	89.464	92.488	<0.001
Reverberation Time	20	174.331	8.717	29.055	<0.001
(2) *Interaction*					
Sound Type x Reverberation Time	*2.804	202.231	*72.124	14.409	*0.001

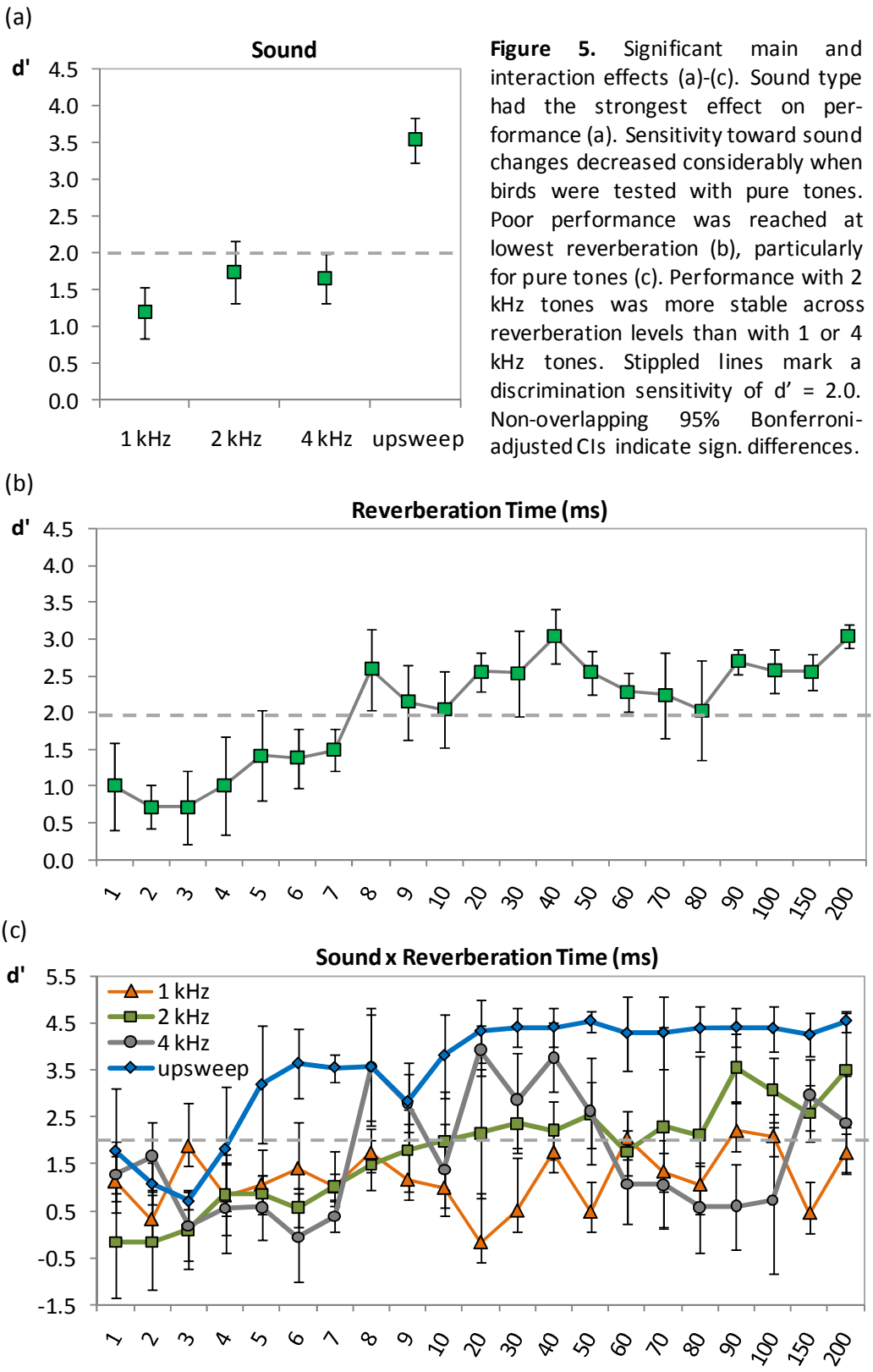


Figure 5. Significant main and interaction effects (a)-(c). Sound type had the strongest effect on performance (a). Sensitivity toward sound changes decreased considerably when birds were tested with pure tones. Poor performance was reached at lowest reverberation (b), particularly for pure tones (c). Performance with 2 kHz tones was more stable across reverberation levels than with 1 or 4 kHz tones. Stippled lines mark a discrimination sensitivity of d' = 2.0. Non-overlapping 95% Bonferroni-adjusted CIs indicate sign. differences.

2. Natural stimuli

Table 3 shows that with natural stimuli the repeated measures ANOVA yielded very similar results for main and interaction effects as with the artificial stimuli reported above. Again, all three main factors (species (SP), sound type (ST), and reverberation time (RT)) had strongly significant effects on the birds' ability to discriminate between non-reverberated and reverberated stimuli, this time with sound type and reverberation level explaining most of the data variation (ST: η^2 = 0.759; RT: η^2 = 0.887 vs. SP: η^2 = 0.620).

Table 3. Repeated Measures ANOVA table showing univariate results for between- and within-subjects effects and their interactions (α = 0.05). The model uses Type III Sums of Squares for balanced designs. *Greenhouse-Geisser adjustment of values where sphericity could not be assumed. Strongest significant effects on performance are (in descending order): reverberation time, sound type, species, and the interaction between sound type x reverberation time. Species is a significant but overall weaker factor.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Between-Subjects*					
Species	2	125.398	62.699	7.348	0.013
(2) *Within-Subjects*					
Sound Type	3	284.583	94.861	28.348	<0.001
Reverberation Time	20	467.930	23.397	70.558	<0.001
(2) *Interactions*					
Species x Sound Type	6	21.141	3.523	1.053	0.414
Species x Reverberation Time	*10.542	15.617	*1.481	1.177	*0.329
Sound Type x Reverberation Time	60	388.250	6.471	22.833	<0.001

Similar to the findings for artificial stimuli (above), post hoc multiple comparisons using Bonferroni adjusted 95% CIs revealed that on average canaries showed a significantly lower perceptual sensitivity (as indicated by the smaller mean value for d') than either of the other two species (Figure 6 (a)), although this difference was

significant only between budgerigars and canaries. Budgerigars, on the other hand, performed best on average but again not significantly better than zebra finches.

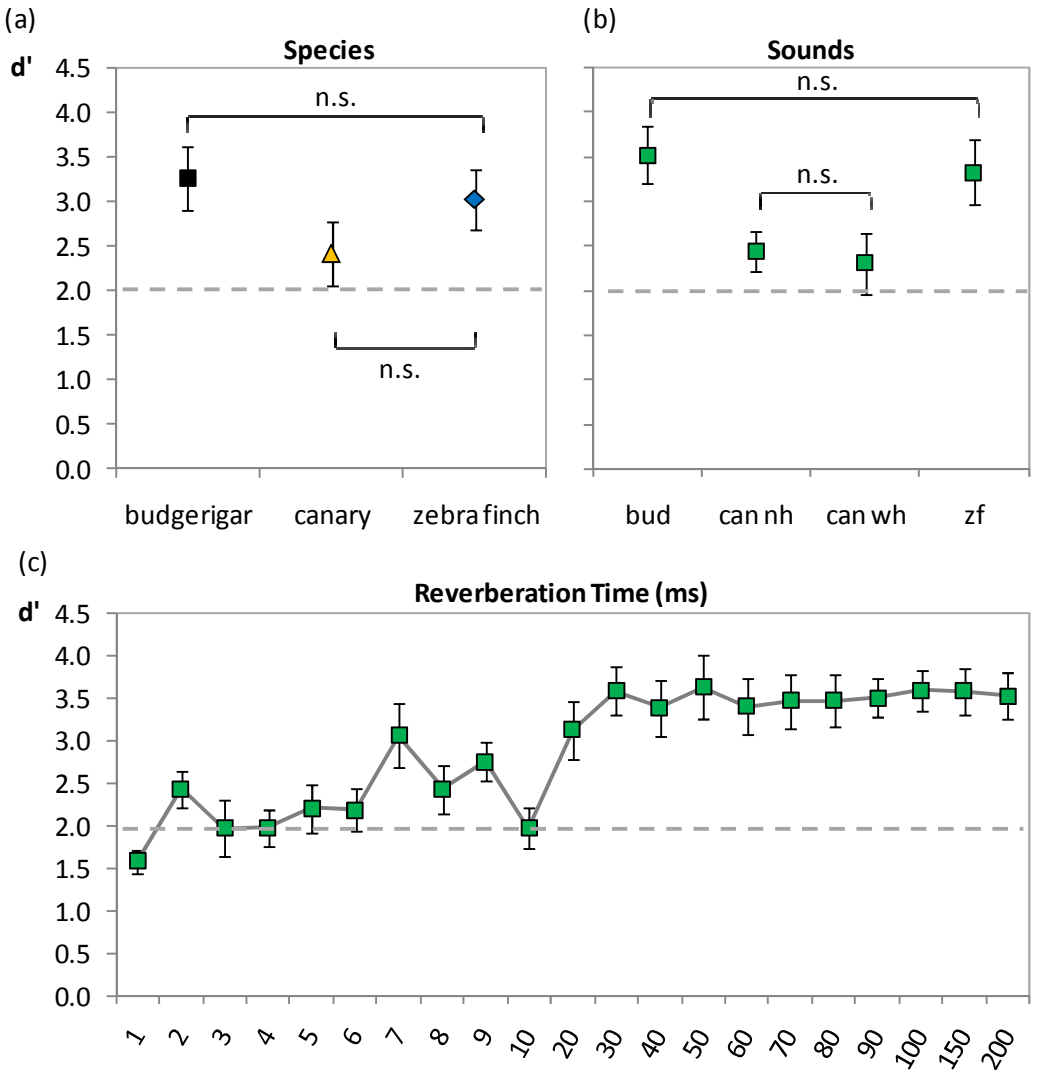


Figure 6. Significant main effects (a)-(c). Budgerigars and zebra finches were most sensitive to sound changes, but performance for all species was well above d' = 2.0 (a). High levels of performance were maintained for all stimuli, although the canary vocalization posed the greatest difficulty (b). Performance at different reverberation times (c) decreased gradually at lower levels but was overall higher than what were seen for artificial stimuli in Figure 3 (c). For factors "species" and "sounds" only non-significant differences between factor levels are marked (n.s.). Significant differences between levels of factor "reverberation time" exist, if the respective 95% Bonferroni-adjusted CIs do not overlap. The stippled lines represent a discrimination sensitivity of d' = 2.0. (bud = budgerigar call, can nh = canary syllable without harmonic, can wh = canary syllable with harmonic, zf = zebra finch syllable)

This difference is also clearly shown in the Figure 7 (a) and (b), which illustrate the performances of all three species with the different sound types and at various reverberation times. In contrast to artificial stimuli, the average performance of all species for natural stimuli was well above moderate levels (d' ≥ 2.0). Comparison of pooled data for different reverberation times (Figure 6 (c)) reveals that performance was never below a d' of 2.0, except at a reverb level of 1 ms. In fact, at lower levels of reverberation (below 20 ms RT) the ability to discriminate between non-reverberated and reverberated stimuli fluctuated somewhat and did not seem to decrease in any discernible pattern. This becomes particularly obvious when comparing results for different stimuli at all reverberation times (Figure 7 (c)). The graph suggests that the average fluctuation below reverberation times of 20 ms seen in Figure 6 (c) was mainly due to the considerable variation of data obtained for the two canary stimuli at those reverberation times. Since the tested canary stimuli resemble a pure tone at a frequency of about 3.1 kHz, it is not surprising to find that the birds' performance with these stimuli are somewhat similar to their performance with the 2 kHz pure tone (or the 4 kHz pure tone) above. While discrimination sensitivity decreases considerably and often below d' = 2.0 at reverberation times less than 20 ms, performance remains rather consistently well above d' = 2.0 for budgerigar and zebra finch stimuli at any reverberation level. This is reflected in the strongly significant interaction effect between sound type and reverberation times (Table 3, Figure 6 (c)). As seen with artificial stimuli, this significant difference in sensitivity could again be explained by the broader

frequency spectrum and the rapid FM and AM of these stimuli compared to the rather pure-tone-like canary syllables.

Although canaries generally were much worse than the other two species at distinguishing between the absence and presence of specific levels of reverberation, they were nonetheless capable of performing this task above d' of 2.0 with all sound types (Figure 7 (a)). Being tested with the canary's own vocalization, however, did not seem to be of any advantage to the birds. Not surprisingly, the preservation of the second harmonic also did not improve their performance because it is at a frequency at which the canaries' auditory sensitivity considerably declines (Figure 1 shows the canary vocalization with the second harmonic at 6.2 kHz). Only budgerigars and zebra finches performed slightly (albeit not significantly) better with their species' own vocalization (SOV).

Reverberation changes were undoubtedly perceived more readily over broad rather than narrow frequency bands. This may be because (a) signals with broader spectra are more susceptible to reverberation-induced alterations in their spectral and temporal patterns, and because (b) birds may use the additional information gathered from the excitation of a larger number of auditory filters. Since auditory filters cover relatively narrow frequency bands (Manley et al. 1989; Langemann et al. 1995), sounds with broad spectra will excite more filters. The auditory system then integrates information from several filters, enhancing the auditory percept of the signal. It is thus possible that this neural mechanism is in part responsible for the improved performance for sounds with broader spectra.

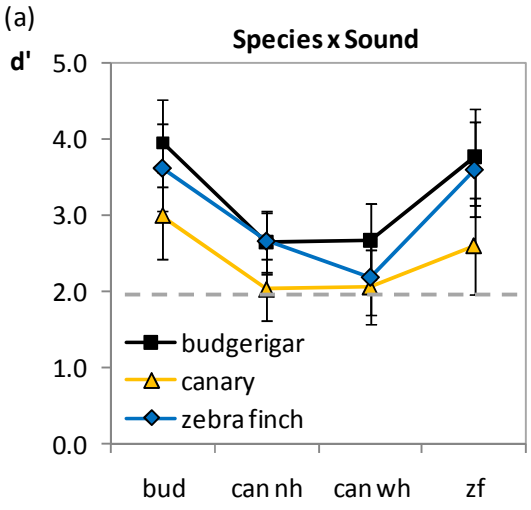
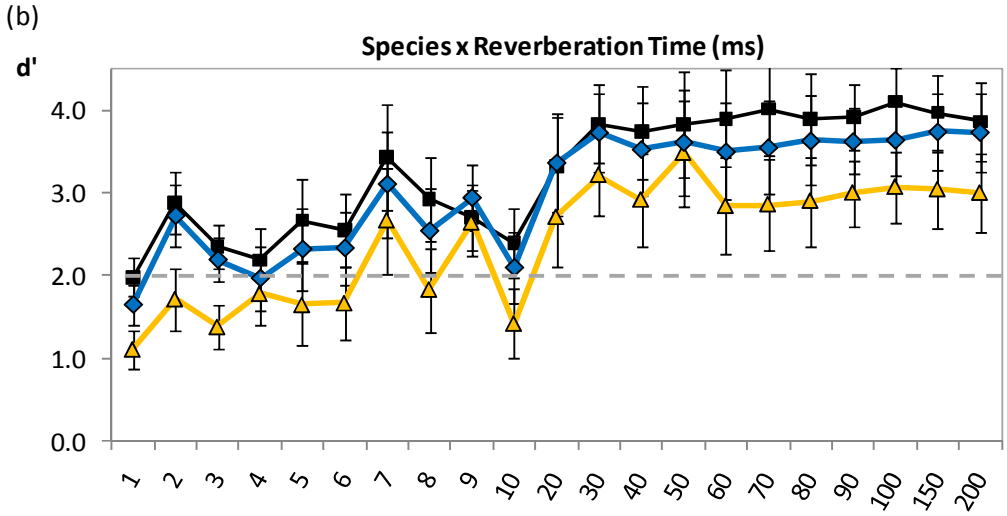
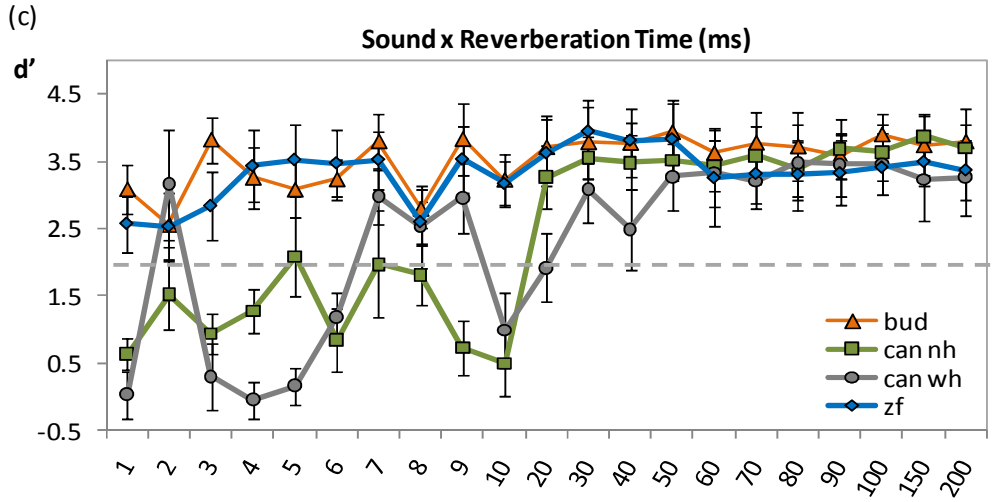


Figure 7. Interaction effects between species and sound (n.s.) (a), species and reverberation time (n.s.) (b) and sound and reverberation time (sign.) (c). (a) and (b) illustrate the canaries' consistently worse performance across all sounds and reverberation times. In contrast to canary vocalizations sensitivity toward reverberation induced changes remained high for the broader-band zebra finch and budgerigar vocalizations even at low reverberation levels. Stippled lines mark a sensitivity of d' = 2.0. Non-overlapping 95% Bonferroni-adjusted CIs indicate significant differences between factor levels.





(bud = budgerigar call; can nh = canary syllable without harmonic; can wh = canary syllable with harmonic; zf = zebra finch syllable)

3. Natural stimuli with noise masker

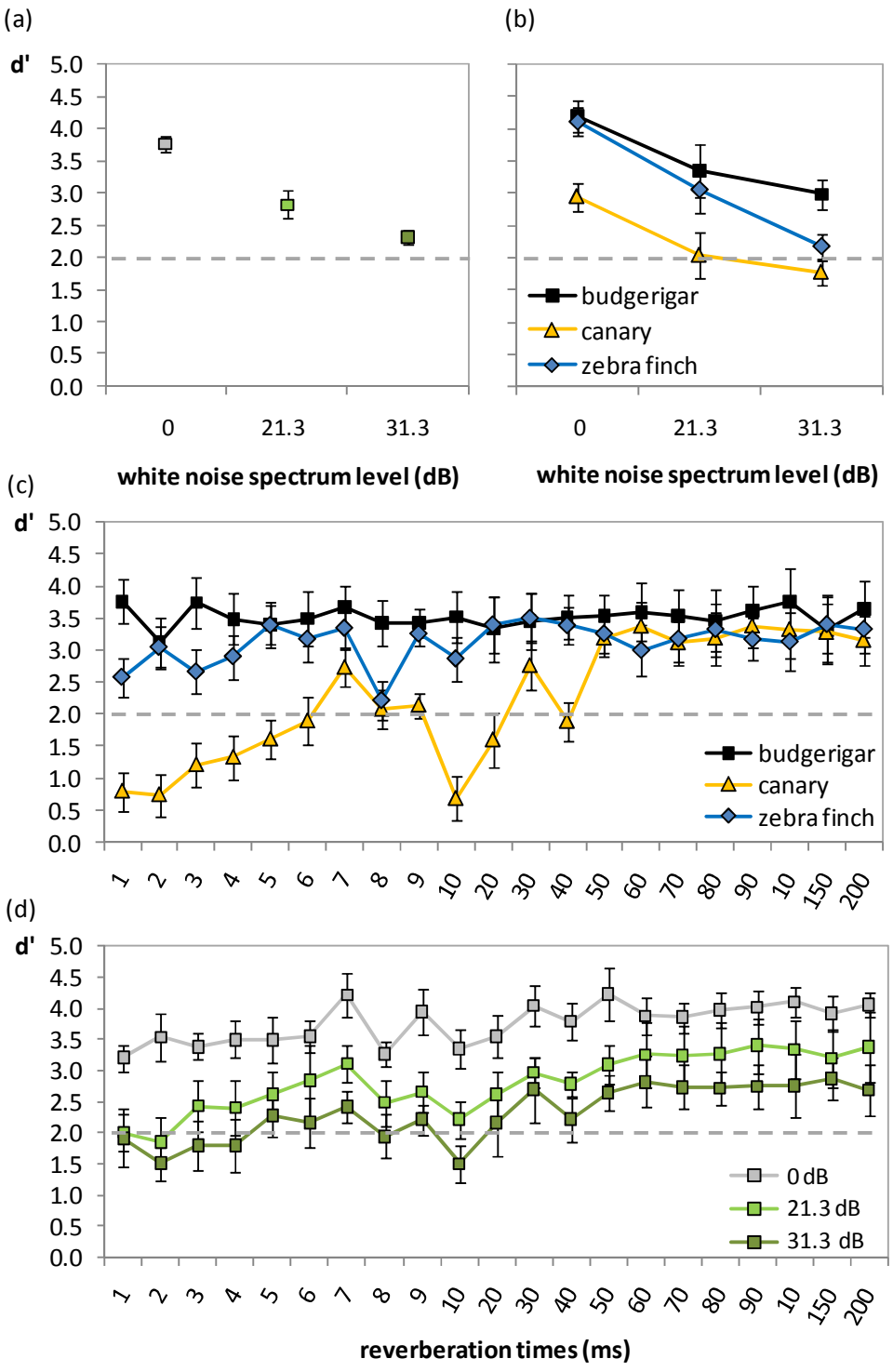
All three main factors (species (SP), noise level (NL), and reverberation time (RT)) had strongly significant effects on the birds' ability to discriminate between non-reverberated and reverberated stimuli (Table 4), this time with species having the strongest effect and explaining most of the data variation, followed by noise level (SP: $\eta^2 = 0.948$; NL: $\eta^2 = 0.939$ vs. RT: $\eta^2 = 0.728$). The relative stronger effect of species as a factor in this experiment compared to the two previously described can be explained by the fact that each species was only tested with their own vocalizations. As seen for experiments with natural stimuli above, canary stimuli caused the greatest difficulty for all species, and canaries did not have any perceptual advantage despite their own species' vocalization.

Table 4. Repeated Measures ANOVA table showing univariate results for between- and within-subjects effects and their interactions ($\alpha = 0.05$). The model uses Type IV Sums of Squares for balanced designs. *Greenhouse-Geisser adjustment of values where sphericity could not be assumed. Noise had the strongest effect, followed by species (own vocalization), reverberation time, and the interaction between species and reverberation time.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Between-Subjects*					
Species (Own Vocalization)	2	187.465	93.733	72.841	<0.001
(2) *Within-Subjects*					
Noise Level	2	243.541	121.771	122.750	<0.001
Reverberation Time	20	98.526	23.070	21.415	<0.001
(2) *Interactions*					
Species (Own V.) x Noise Level	*2.727	16.749	*6.141	4.221	*0.035
Species (Own V.) x Reverb. Time	40	133.397	3.335	14.497	<0.001
Noise Level x Reverb. Time	*4.638	12.397	*2.673	1.330	*0.275

Performance differences between canaries and the other two species therefore were likely emphasized by this experimental design. Similarly, budgerigars and zebra finches were tested with their own stimuli, with which they had shown to perform best, additionally enhancing the species difference in overall performance. Overall this resulted in an average d' of 3.51 ± 0.19 for budgerigars, 2.26 ± 0.17 for canaries, and 3.117 ± 0.17 for zebra finches (mean with 95% CI limits), which were all significantly different from each other according to multiple comparisons using Bonferroni-adjusted 95% CIs. The difference between canaries and the other two species is also clearly illustrated in Figure 8 (b) and (c), which show the significant interaction effects of species with both noise level and reverberation level. Independent of reverberation or noise level, budgerigars and zebra finches always retained their ability to discriminate reverberated from non-reverberated stimuli above d' = 2.0, whereas the canary's performance clearly dropped below that value at the highest noise spectrum level and at reverberation times of 10, 20, and 40 ms,

Figure 8 (next page). Main and interaction effects showing 95% Bonferroni-adjusted confidence intervals around estimated marginal means (a)-(d). Only noise level as significant main factor is shown (a). Significant interaction effects are between species and noise (b) and species and reverberation (c) but not between noise and reverberation (d). Noise had a great impact on performance (a), especially for zebra finches who exhibited the greatest relative decline in sensitivity (a maximum change in d' of 1.95) (b). Zebra finches and budgerigars have a high and nearly unchanged performance across all reverberation times, whereas the canaries' sensitivity changes considerably (declines in d' up to 2.25) (c). (d) shows that differences in performance between noise levels are rather consistent across reverberation *times*. Stippled lines mark a discrimination sensitivity of d' = 2.0, equivalent to moderate performance levels. Non-overlapping CIs indicate significant differences between factor levels.



and again below 7 ms. Interestingly, in comparison with other species, it is the zebra finch whose performance decreased most from conditions without noise to those with the highest noise level. The main characteristic features of this species'

vocalizations (including the syllable used in this experiment) are their 'noisiness', which is brought about by the broad spectral spread of the sound energy, the strongly harmonic structure and the rapid amplitude modulations. It would make sense, therefore, for white noise to have a greater masking effect on stimuli that more closely resemble the noise masker itself than on stimuli that are more tonal in character, especially if the feature to distinguish is the presence or absence of reverberation-induced signal alterations.

EXPERIMENT 2 – NATURAL SCATTERING:

1. Object – rectangular box

Species (SP), sound type (ST), and box placement (BP) all had a significant effect on the birds' performance (Table 5). Species and the presence and position of the box explained most of the variation in the dataset (SP: $\eta^2 = 0.915$ and BP: $\eta^2 = 0.877$ compared to vs. ST: $\eta^2 = 0.622$). Birds were clearly capable of hearing the difference between the absence and presence of the box (Figure 9 (c)), although budgerigars and zebra finch were better at this task than canaries, whose sensitivity toward these differences were just above d' = 1.0 (Figure 10 (b)). In contrast to the experiments describe above, I chose a d' of 1.0 as performance level against which to compare the results instead of the more conservative d' = 2.0, because this task was a great deal more difficult, and a d' of 1.0 still corresponds to a moderate performance of 50% hits and 16% false alarms (see 2.2.5 "Measuring Auditory Sensitivities in the Lab"). A higher level would have obscured the more subtle discrimination abilities of these birds that were nonetheless significantly dependent

on the tested factors and some of their interactions. The predominant frequency range covered by the sounds is between 1 and 4 kHz, which is equivalent to sound wavelengths between 34 and 8.5 cm (at 20°C). An object of the size as the one used in this experiment therefore can easily obstruct sounds that fall within that range. In contrast, the birds showed much less sensitivity toward changes in just the position of the box, especially when the change was from an angle of 0° to 45° relative to the sound transmission pathway (see Appendix IV for an illustration of position changes). This could be because position changes from 0° to 45° still allow for much of the box's surface area to obstruct the transmission pathway and scatter sound waves, whereas moving the box from 0° to 90° imply a change to a much smaller surface area that is orthogonal to the direct sound path (from 0.14 m^2 to 0.09 m^2). Here, the performance of the three species did not differ much, all approaching d' = 1.0. This change in performance difference between the species as seen in Figure 10 (b) accounted for the significant interaction effect between species and object placement (Table 5). The overall difference between species is shown in Figure 9 (a). Budgerigars were significantly more sensitive than canaries toward sound changes brought about by the presence and position of an object in the pathway. Sound type, too, was a significant contributor to the performance of the birds (Table 5), although there was no apparent species-specific advantage in being tested with the species' own vocalization (Figure 10 (a)). Only the difference between the canary and zebra finch syllables were significant according to post-hoc Bonferroni-adjusted multiple comparisons, with zebra finch syllables being easiest

(Figure 9 (b) and 10 (c)). There is also a tendency for birds to more readily distinguish changes in the zebra finch syllable than the budgerigar call. The reason

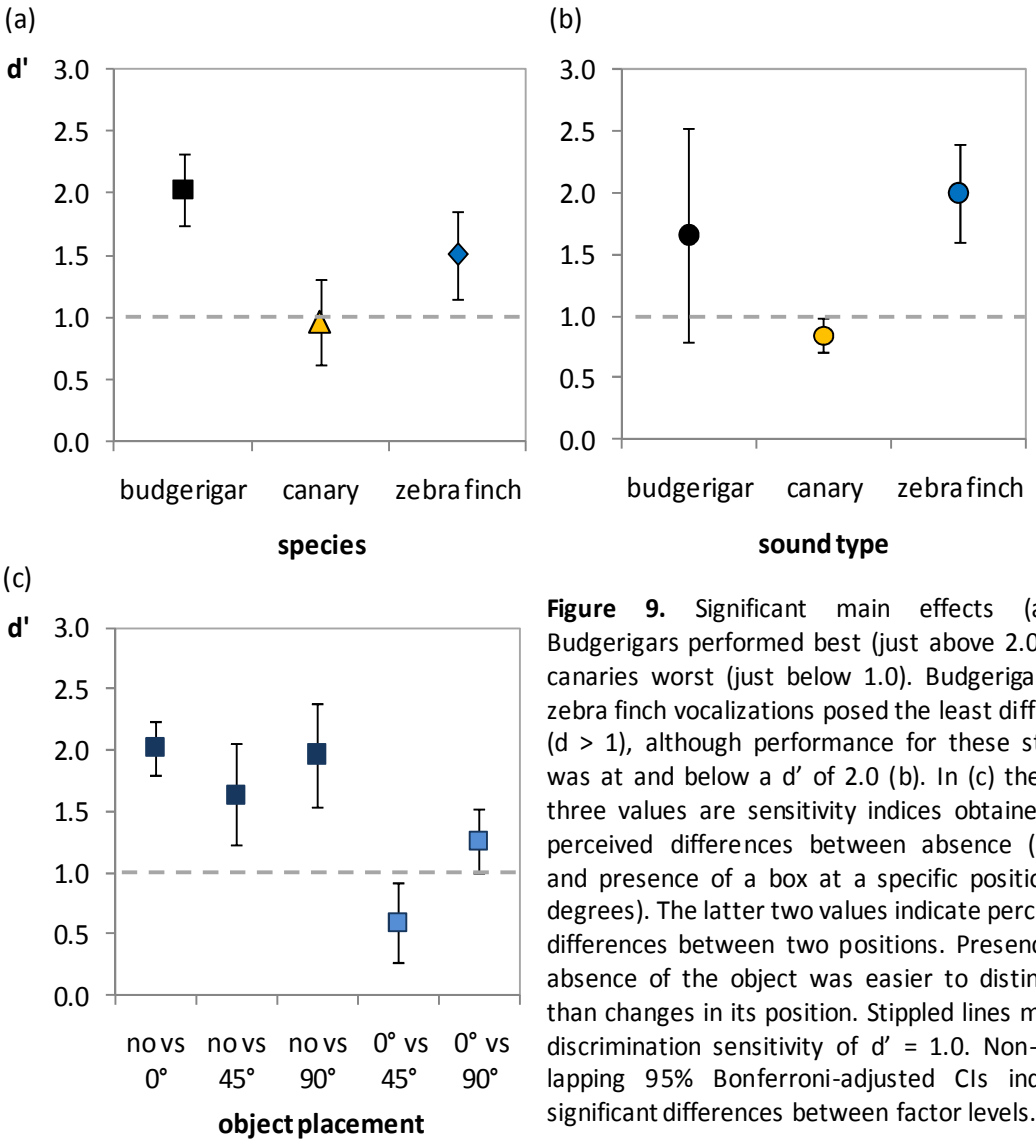


Figure 9. Significant main effects (a)-(c). Budgerigars performed best (just above 2.0) and canaries worst (just below 1.0). Budgerigar and zebra finch vocalizations posed the least difficulty (d > 1), although performance for these stimuli was at and below a d' of 2.0 (b). In (c) the first three values are sensitivity indices obtained for perceived differences between absence ("no") and presence of a box at a specific position (in degrees). The latter two values indicate perceived differences between two positions. Presence vs. absence of the object was easier to distinguish than changes in its position. Stippled lines mark a discrimination sensitivity of d' = 1.0. Non-over-lapping 95% Bonferroni-adjusted CIs indicate significant differences between factor levels.

Table 5. Repeated Measures ANOVA table showing univariate results for between- and within-subjects effects and their interactions (α = 0.05). The model uses Type III Sums of Squares for unbalanced designs. Strongest significant effects on performance are (in descending order): box placement, interaction between box placement and sound type, and species.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Between-Subjects*					
Species	2	20.781	10.390	21.652	0.007
(2) *Within-Subjects*					
Sound Type	2	23.700	11.850	6.586	0.020
Box Placement	4	28.155	7.039	27.303	<0.001
(2) *Interactions*					
Species x Sound Type	4	12.898	3.225	1.792	0.224
Species x Box Placement	8	8.310	1.039	4.029	0.009
Sound Type x Box Placement	8	44.954	5.619	18.072	<0.001

is again likely to be found in the much broader spectral make-up of the zebra finch vocalization compared to any of the other two vocalization types. When sound waves are reflected and refracted in the presence of an obstacle in the pathway, the resulting structural alteration to the sound are frequency-dependent. Therefore, signals with acoustic energy spread across a broad range of frequencies will likely exhibit more degradation than sounds with a more limited frequency range. Moreover, amplitude modulation patterns are highly affected by reverberation, and sound rich in AM (such as zebra finch syllables) will experience greater degradation as a result than sounds with much less AM. This apparently greater susceptibility of the zebra finch syllable to degradation and the resulting audible signal changes cannot explain, however, why we see the strongly significant interaction effect between sound type and box presence/position (Table 5, Figure 10 (c)).

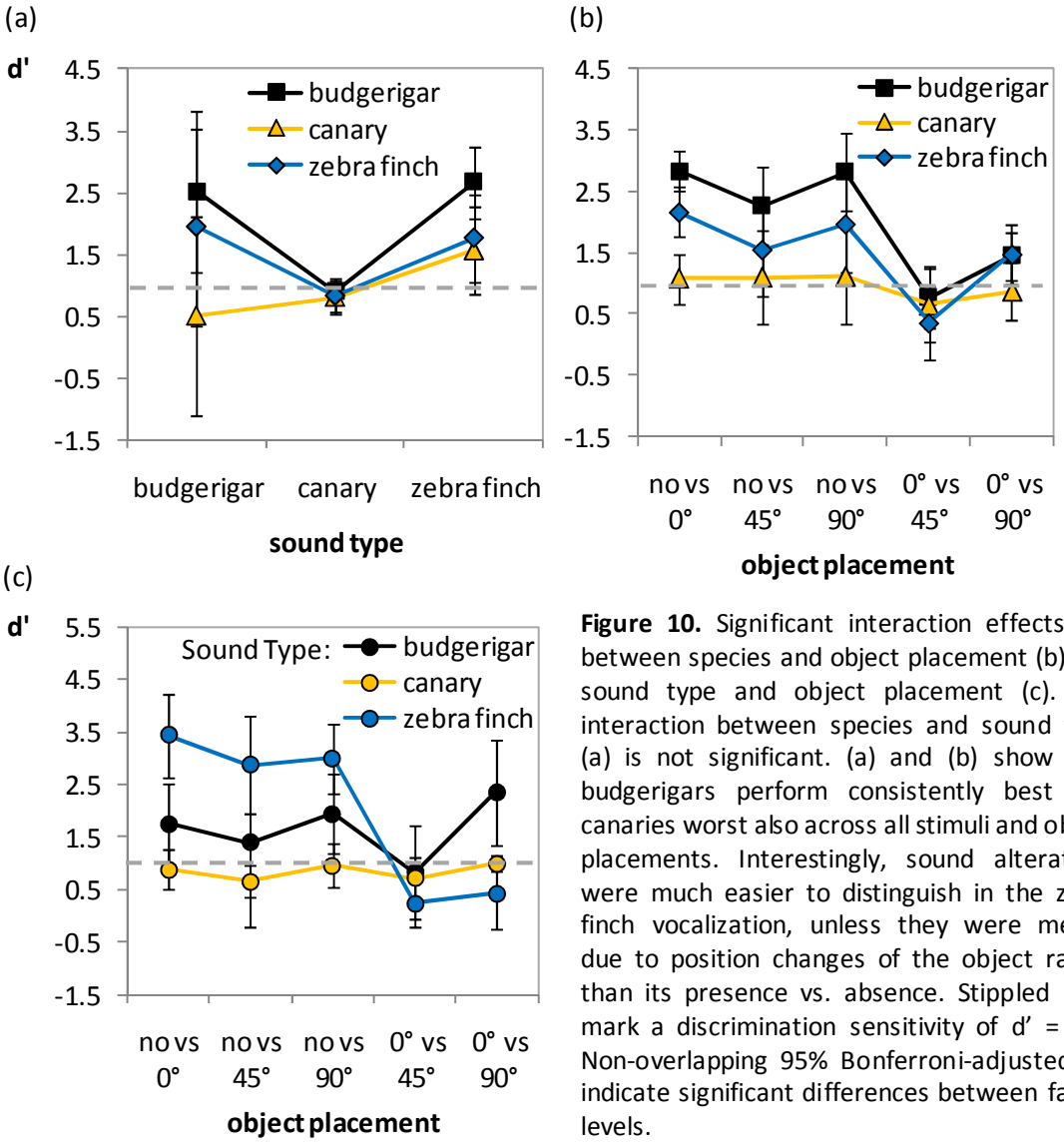


Figure 10. Significant interaction effects are between species and object placement (b) and sound type and object placement (c). The interaction between species and sound type (a) is not significant. (a) and (b) show that budgerigars perform consistently best and canaries worst also across all stimuli and object placements. Interestingly, sound alterations were much easier to distinguish in the zebra finch vocalization, unless they were merely due to position changes of the object rather than its presence vs. absence. Stippled lines mark a discrimination sensitivity of d' = 1.0. Non-overlapping 95% Bonferroni-adjusted CIs indicate significant differences between factor levels.

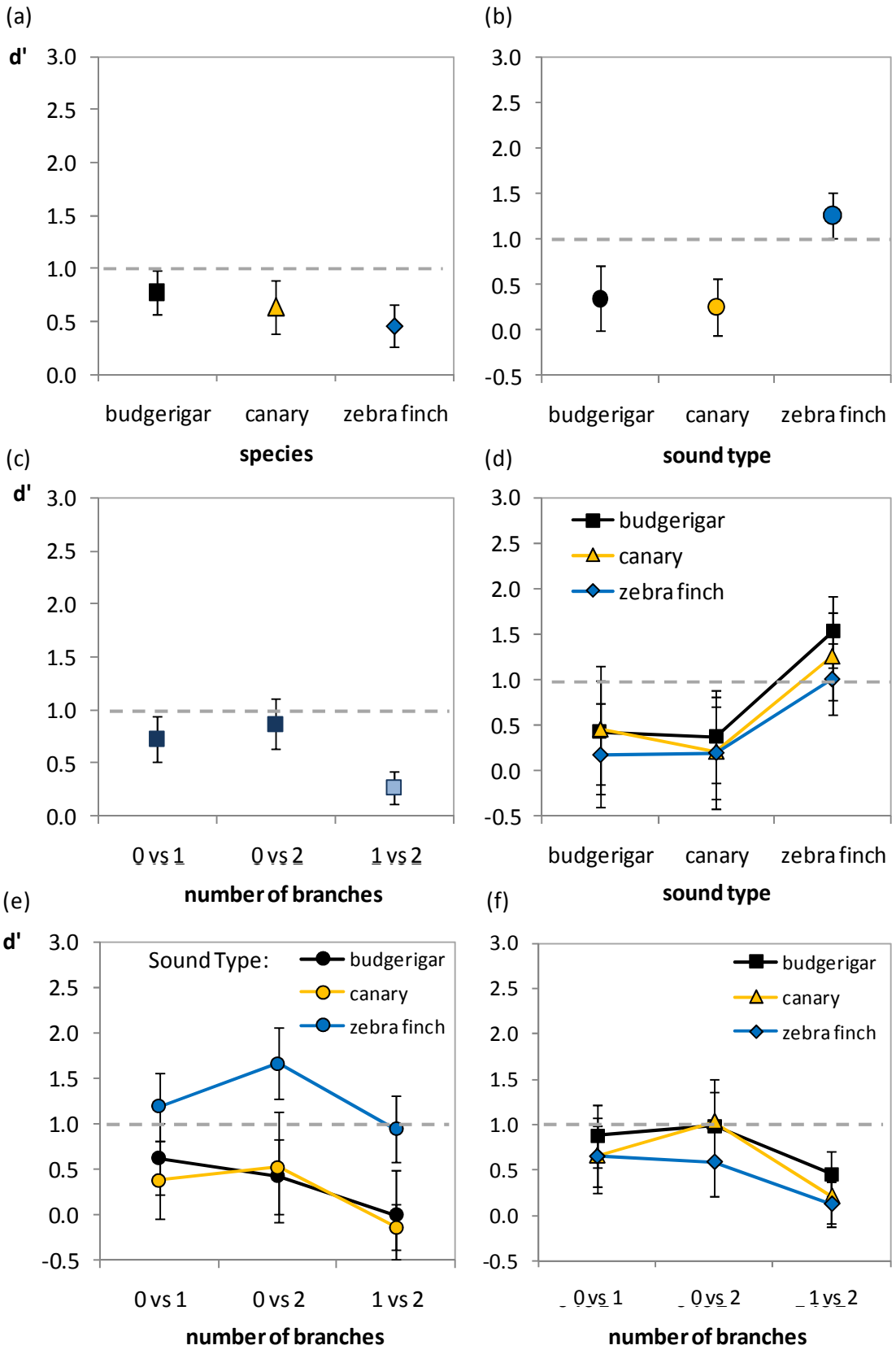
2. Object – tree branches

Only the two within-subjects effects (sound type and tree branch presence/number) were in fact significant (Table 6), both being almost equally responsible for the observed variation in the dataset (ST: $\eta^2 = 0.775$ and BP: $\eta^2 = 0.772$). Generally, all species performed just below d' = 1.0 (Figure 11 (a)), except when the tested sound was the zebra finch syllable (Figure 11 (b), (d), and (e)), in which case budgerigars were slightly better than the other two species at hearing

Table 6. Repeated Measures ANOVA table showing univariate results for between- and within-subjects effects and their interactions (α = 0.05). The model uses Type III Sums of Squares for unbalanced designs. Factors with strongest significant effects on performance are (in descending order): sound type and tree presence/number.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Between-Subjects*					
Species	2	1.348	0.674	4.077	0.089
(2) *Within-Subjects*					
Sound Type	2	14.536	7.268	17.244	0.001
Tree Presence/Number	2	4.594	2.297	16.905	0.001
(2) *Interactions*					
Species x Sound Type	4	0.426	0.106	0.252	0.902
Species x Tree Presence/N umber	4	0.401	0.100	0.737	0.587
Sound Type x Tree Presence/Number	4	0.897	0.224	1.530	0.232

Figure 11 (next page). Main effects species (a), sound type (b), and tree branch number (c) as well as interaction effects between the three factors (d-f) showing 95% Bonferroni-adjusted confidence intervals around estimated marginal means. Of all main and interaction effects only (b) and (c) were significant. All species had performance level below 1.0 (a). There was also no consistent pattern among species across different vocalizations or branch density (d)+(f). (b) and (d) clearly show that scattering-induced differences in zebra finch vocalizations were more easily discriminated (d' > 1.0) than differences in the other vocalizations (d' < 1.0). Stippled lines mark a discrimination sensitivity of d' = 1.0. Non-overlapping CIs indicate significant differences between factor levels.


(a)
d'
3.0
2.5
2.0
1.5
1.0
0.5
0.0
budgerigar
canary
zebra finch
species
(b)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
budgerigar
canary
zebra finch
sound type
(c)
d'
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0 vs 1
0 vs 2
1 vs 2
number of branches
(d)
budgerigar
canary
zebra finch
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
budgerigar
canary
zebra finch
sound type
(e)
d'
Sound Type:
budgerigar
canary
zebra finch
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
0 vs 1
0 vs 2
1 vs 2
number of branches
(f)
budgerigar
canary
zebra finch
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
0 vs 1
0 vs 2
1 vs 2
number of branches

the differences caused by the presence of tree branches. Again, it is possible that the broad spectral and harmonic character of the zebra finch sound compared to the other tested stimuli renders it more susceptible to object-induced scattering and poses an advantage to the birds in detecting sound changes (see discussion above). The presence of tree branches caused hardly any audible differences in the structural details of the sound signals, likely because obstructing surfaces such as holly leaves and twigs were rather small and, because of natural branch growth, randomly placed. Yet, sound degradation caused by the addition of two branches (rather than just one) could be heard more easily when compared to a non-degraded sound, and average performance of the birds in fact approached moderate levels (d' = 1.0) (Figure 11 (c)). However, this is only true for the canaries and budgerigars (Figure 11 (f)). Surprisingly and contrary to the results reported in any of the previous experiments above, the zebra finch and not the canary tends to be least sensitive to these changes. This difference, however, is not significant. One should also bear in mind, though, that in natural environments signal changes accumulate over distance and across a multitude of reflective surfaces, so my experiments with different objects test a quite unique and perceptually less common situation, and it is likely that results would be quite different if larger distances and more objects were used.

EXPERIMENT 3 – STRUCTURALLY DECOMPOSED STIMULI

Non-random noise substitution

The purpose here was to compare the performance of birds with the original natural stimuli and non-random noise that contained the amplitude envelope function of these stimuli. The substitution of the fine structural details of the previously tested natural stimuli with non-random white noise preserved their overall envelope function. It assured that the only difference audible to the birds would be differences in the envelope (or amplitude fluctuations) caused by reverberation. Once all reverberated natural stimuli were substituted with noise and their respective envelope function, I was able to test whether the seemingly easy distinction between non-reverberated and reverberated sounds seen in Experiment 1 was based on changes in the overall amplitude modulation patterns alone.

The results suggest that the changes in the envelope function of a sound indeed played a significant role in correctly detecting changes brought about by reverberation (Figure 12 (d)). A comparison between the performances with natural and noise-substituted stimuli revealed a significant difference between the two in the percentage of correct responses given to perceived changes between non-reverberated and reverberated sounds (Wilcoxon Signed Rank; budgerigar sounds: $Z = -2.506$, $P = 0.012$, $N = 210$; zebra finch sounds: $Z = -3.377$, $P = 0.001$, $N = 210$). Despite this significant difference, noise-substituted stimuli that only contained reverberation cues in the envelope function of the sounds were nonetheless very

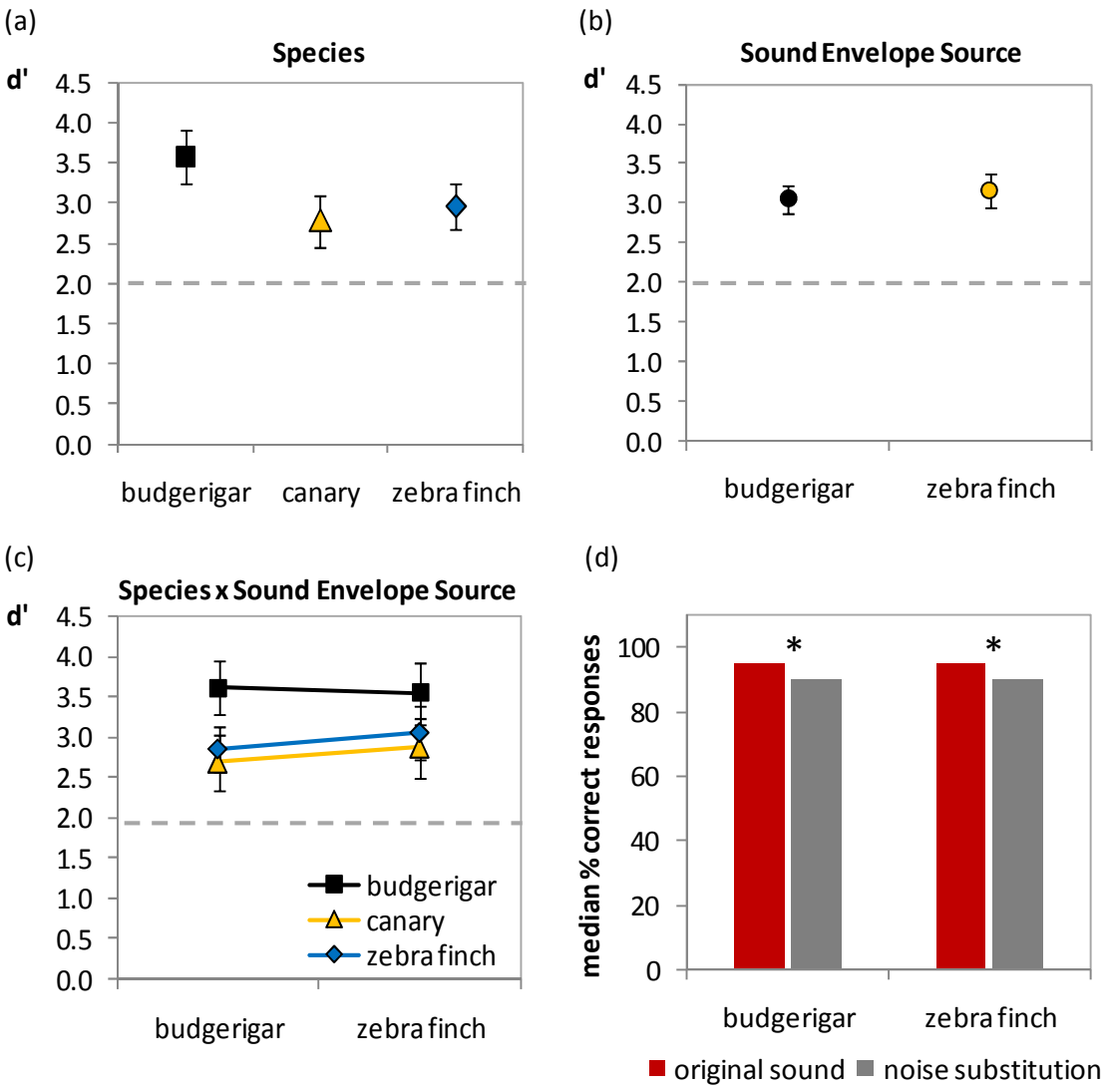


Figure 12. Performance of different species (a) and with different sounds (b). The sensitivity of each species with regard to the sound type is shown in (c). Here, results are expressed as sensitivity index d' for easy comparison, with stippled lines marking a discrimination sensitivity of d' = 2.0. Budgerigars performed best and canaries worst (a)+(c), but average performance was well above 2.0 for all species and conditions. Sounds were equally easy to distinguish independent of sound envelope source (b). In (d) median percentage of correct responses is compared between the original stimuli and their noise substitution. Original stimuli were the budgerigar call and the zebra finch syllable tested in Experiment 1 of this study. Noise substitutions were non-random noise bands with the imposed envelope function of each reverberated and non-reverberated natural sound. Although differences in performance were significant between original and noise-substituted stimuli, correct responses to noise substitutions were still given on average on 90% of all trials while false alarm rate stayed constant. Significant differences in (d) are marked with *. Bars represent 95% Bonferroni-adjusted confidence intervals in (a)-(c).

easy to discriminate for all tested species independent of stimulus type (Figure 12 (a), (b)). Expressed as % correct responses, the overall difference amounted to only 5% for both zebra finch and budgerigar stimuli (median: 95% vs. 90%). While audible differences in the envelope function alone seem to suffice, additional changes in for example the frequency spectrum or other fine structural changes such as phase shifts may potentially be used and could account for the improvement in performance when birds were tested with the natural stimuli. It would, however, be necessary to conduct these noise substitution tests with other reverberated natural stimuli that posed much greater difficulty in the distinction of absent and present reverberation. It is conceivable that with increased difficulty of the task, the envelope alone may not provide sufficient information and other, more reliable, cues are used. Such cues could be found in other aspects of the temporal or frequency patterns of the sounds.

3.1.4 GENERAL DISCUSSION

This study aimed to provide a broader understanding of the perceptual implications of reverberation and other forms of sound scattering by testing birds with a wide variety of acoustic stimuli and reverberation- or scattering-induced alterations. By including very small levels of reverberation and scattering I hoped to reveal the perceptual limits of the test subjects' auditory systems. I focused on the differences in sound degradation that are perceivable via changes in the acoustic structure of a transmitted signal and the potential usefulness of these differences in distance

estimation or evaluation of the acoustic environment. Another important aspect of this study was to determine the perceptual sensitivity of the three species' auditory systems and reveal potential species-specific adaptations to reverberation- and scattering-induced signal alterations. Addressing these simpler questions was also necessary before engaging in the investigation of more complex perceptual tasks regarding communication in reverberant environments such as the ones described later in this dissertation.

The results suggest a species- and stimulus-dependent ability to discriminate between non-reverberated and reverberated sounds and different levels of object-induced sound scattering, even when either effects are small. Generally speaking, the individual findings can be understood in terms of what is already known about the auditory capabilities of the individual species, with few exceptions. A previous comparative study with budgerigars and zebra finches, for example, demonstrated that each species processes its own species' vocalizations most efficiently (Dooling et al. 1992). The present findings do not support my hypothesis that this is also true for tasks involving the detection of reverberation and scattering differences. There are seemingly no species-specific adaptations to the properties of the species' own vocalizations that would result in a perceptual advantage for detecting the induced signal changes. Canaries generally performed worst and budgerigars best (followed by zebra finches), independent of stimulus type. However, budgerigars are known to have an exceptionally high spectral resolving power at 2.86 kHz. It is much greater than the resolving power of canaries

and zebra finches at this frequency and in fact close to that of humans (Okanoya and Dooling 1987). Therefore, from a purely psychoacoustic perspective the higher sensitivity of budgerigars seen in this study is hardly surprising, given that reverberation- and scattering-induced changes affect both the temporal and spectral patterns of the sounds. Zebra finches were very close to budgerigars in their auditory sensitivity toward these changes, and in the majority of cases the slight differences between them were not significant. Their auditory system has an extraordinarily high temporal resolving power that allows them to detect phase shifts based on temporal cues alone (Dooling et al. 2002; Dooling and Lohr 2006). This ability may have enhanced the perception of reverberation and other types of sound scattering, both of which introduce phase shifts due to the interactions between direct and reflected waves. Given that budgerigars and zebra finches performed much better in these tasks compared to canaries, this part of the study could be evidence that changes in either the spectral or temporal patterns of a signal are sufficient in discriminating different degrees of reverberation and scattering. In fact, in the case of artificial reverberation this study has demonstrated that if only changes in the overall envelope (i.e. AM patterns) are preserved as a cue, birds have no difficulty in discriminating non-reverberated from reverberated stimuli. On the other hand, reverberation and especially sound scattering also likely affect a vocalization's timbre, which is determined by the relative amplitude of the sound's frequency components. Zebra finches, for instances, can discriminate differences in timbre of their vocalizations (Cynx et al. 1990), and it could be argued

that the more varied the power spectrum, the more likely it is for reverberation and sound scattering to cause changes in timbre that could serve as yet another cue. Also important could be the zebra finches' and budgerigars' enhanced ability to detect changes in the harmonicity of complex harmonic stimuli compared to humans, and their exceptional sensitivity toward subtle changes of even a single harmonic (Lohr and Dooling 1998). The underlying mechanisms responsible for this sensitivity could arguably be the cause also for these two species' much enhanced ability to detect reverberation- and scattering-induced differences compared to canaries, especially with highly harmonic stimuli. This greater sensitivity could then imply that either these mechanisms are different from the ones used by canaries or are the same but simply less crude in the discrimination of the available cues. Interestingly, in experiments with the species' own vocalizations and different background noise levels, it was the zebra finches whose ability to discriminate suffered relatively more from the addition of a white noise masker than the other two species, possibly as a result of the very broadband, harmonic structure of the sounds. The broad frequency spectrum lends a somewhat noisy quality to the sounds, and alterations in the harmonicity or timbre of highly harmonic stimuli (as could be expected from reverberation and scattering) changes their noisy character by introducing phase shifts (Hartmann 1988). Such changes, however, may get easily lost in noise that is itself characterized by random phases. Furthermore, it has been argued that avian perception of subtle changes in harmonicity (i.e. mistuned harmonics) is dependent on background noise levels (Lohr and Dooling 1998). It is

thus not surprising that differences in the already noisy quality of zebra finch vocalizations (brought about by changes to its harmonic structure) would get slightly lost in the presence of a white noise masker with a similarly broad spectrum. Greater spectral resolving power conceivably could have mitigated these effects somewhat.

The width of the frequency spectra of the stimuli and the overall spectral patterns clearly played an important role in determining the sensitivity of the birds toward reverberation- and scattering-induced signal alterations. All artificial pure tones or pure-tone-like natural vocalizations were generally harder to discriminate than any of the other stimuli tested in this study. Apart from the perceptual considerations discussed above, the improved performance with broad-spectral sounds could also be attributed to specific excitation patterns they cause on the basilar papilla. A broader frequency range excites a larger area on the basilar papilla, thus covering a large number of frequency filters from which information can be obtained and integrated to form a complete percept of reverberation. Moreover, sounds with broader spectra are more susceptible to degradation and thus more likely to accumulate structural changes caused by reverberation and scattering. When the tested sounds were pure tones, sensitivity also appeared to be determined by the frequency of the sound relative to the frequency of best hearing in birds. Structural differences in tones at 2 kHz were easier to distinguish than in a 1 or 4 kHz tone, which corresponded well with the three species'

frequency region of best absolute auditory sensitivity between 2 and 3 kHz (Dooling 1982; Dooling 2004).

Taken together, there is evidence to suggest that any kind of scattering, including reverberation, is particularly audible to the birds if sounds contain features that promote degradation, such as broad spectra, a strongly harmonic structure, or considerable AM or FM. The typical repertoire of each of these species does contain signals that incorporate some or all of these features, and in a given biological context the signaling bird could conceivably make certain signal choices to enhance the perception of degradation at the receiver's end or to reduce the active space of the signal. Canaries, for instance, are famous for the long sequences of trills that are invariably part of their song. They are characterized by a quick succession of very brief song elements that resemble short up- or down-sweeps, resulting in rapid AM and FM throughout the trill sequence. In field studies with rufous- and white-wren song degradation of trills was severe in comparison with other song syllables (Barker et al. 2009). Clearly, such trills would permit quite accurate estimations regarding the amount of reverberation for example (Wiley and Godard 1996). The temporal spacing and number of elements would determine at which reverberation and scattering levels (and corresponding distance or environmental characteristic) single elements and their fine structural details are no longer discernible. Moreover, zebra finches and budgerigars produce rather complex vocalizations with consistent amplitude profiles (Williams et al. 1989; Farabaugh 1998) that are susceptible to the effects of reverberation and scattering.

Here, the capacity to detect changes in timbre caused by an altered amplitude profile could be of great importance in the perception of such environmental effects.

Results from experiments using white noise with the imposed envelope function of natural vocalizations indicated that AM (or the temporal envelope) is pivotal in the discrimination of reverberation, which may be due to the birds' high temporal resolving power (Dooling et al. 2002; Dooling and Lohr 2006). Changes to the overall signal envelope thus play an important but possibly not exclusive role. AM resolution in separate frequency bands, which correspond with the respective species' auditory filter bandwidths, may in fact be of greater importance, especially when the detection of structural changes becomes more difficult. It is also worth noting that imposing the noise with the *average* envelope function of a signal results in an equal representation of the overall AM across the *entire* frequency spectrum, which may have emphasized subtle differences in AM patterns over time. The goal of ongoing experiments with white noise filtered by several bands that represent species-typical frequency channels is to elucidate the role of AM resolution versus spectral resolution in this discrimination task.

It is clear that all three species of birds, particularly the zebra finch and budgerigar, were highly capable of hearing even very small reverberation- and scattering-induced differences in the majority of tested stimuli. Not only were highly controlled levels of artificial reverberation audible to the birds, but also very subtle sound changes brought about naturally by sound waves reflected and

refracted off of objects in the transmission pathway. Based on these first experiments, it is therefore safe to say that the three tested species have the perceptual potential to use perceived reverberation and scattering differences in the judgment of for instance the distance of a sound source and the quality of the surrounding acoustic environment in which signals are emitted. The ability to use reverberation as an absolute and relative distance cue has been demonstrated in humans (von Békéksy 1960; Mershon and King 1975). Whether birds indeed exploit this potential in biologically relevant behavioral contexts, however, is difficult to investigate reliably in either field or lab settings and therefore still remains an open question. The next study in this dissertation attempts to assess whether reverberation can be categorized across different stimuli based simply on the amount of structural changes within the signal and signal elongation by echoes.

3.2 Study II

Categorization of reverberation across vocalizations – Implications for estimating the distance of signalers via stimuli of different familiarity

3.2.1 INTRODUCTION

In animal communication, social network environments play an important role in facilitating the exchange of social information. Many of the vocally-mediated activities in networks particularly involve encoding and extracting information about the signaler itself, such as its identity, status, and intention ('internal state') as well as its location in relation to others ('external state'). Most network activities, however, are limited by the degradation of signals that occurs when those signals travel from sender to receiver, while other activities, such as estimating the distance of a sound source, may not. The degree to which sounds degrade is dependent not only on the properties of the signal and the physical quality or climatic conditions of the environment but also on the distance between the signaler and receiver as well as their relative position towards each other (Waser and Brown 1986; Wilczynski et al. 1989; Dabelsteen et al. 1993; Brown et al. 1995; Mathevon et al. 1996; Holland et al. 1998; Nelson and Stoddard 1998; Blumenrath and Dabelsteen 2004; Blumenrath et al. 2004; Lampe et al. 2004; Mathevon 2005; Barker et al. 2009). Indeed, by attending to the received version of a vocalization many animals seem to be able to judge the distance to and direction of a vocalizing conspecific, an activity commonly termed 'ranging' (e.g. Michelsen and Larsen 1983; McGregor and Falls 1984; McGregor and Krebs

1984; Klump et al. 1986; Shy and Morton 1986; Wilczynski and Brenowitz 1988; Brenowitz 1989; McGregor and Krebs 1989; McGregor 1994; Klump 1996a; Naguib 1996b; Fotheringham et al. 1997; Naguib 1997; Nelson and Stoddard 1998; Holland et al. 2001a; Brumm and Naguib 2009). This auditory distance assessment facilitated by sound degradation is particularly important in situations when the optimal initial response to a signal depends on the distance of the signaler, such as in territorial disputes. While the ability of animals to judge the distance of a signaler based on degradation cues is well-documented particularly in birds, the question of exactly which type of cues are used has been a subject of great debate. This debate has been fueled in part by contradictory evidence from field studies showing that either attenuation, reverberations added to the signal as tails of echoes, or location-specific cues such as off-axis and near-axis reflections are used (Naguib 1995; Morton 1998; Naguib 1998; Nelson and Stoddard 1998; Naguib et al. 2000; Nelson 2000; Holland et al. 2001a; Holland et al. 2001b). So far, however, only one field study with the wren (*Troglodytes troglodytes*) has investigated the role of structural changes within the original time frame of the signal in combination with echo elongations (Holland et al. 2001a; Holland et al. 2001b). The modified song structure (Mathevon and Aubin 1997; Holland et al. 2001a), but also the change in sound pressure level or amplitude (Naguib 1997; Nelson 2000) seem to provide distance cues to the receiver that can be used in ranging, although the latter is somewhat subject to manipulation by the signaler who can adjust signal loudness in response to transient fluctuations in background

noise, known in many species as the Lombard Effect (Lombard 1911; Pick Jr et al. 1989; Manabe et al. 1998; Junqua et al. 1999; Brumm and Todt 2002; Brumm 2004; Egnor and Hauser 2006). In transmission studies with great tit *Parus major* songs, it was shown that distortions within the signal, the relative energy of the echo tails, and the echoes' energy decline rate changed significantly with distance (Blumenrath and Dabelsteen 2004). While varying predictably with distance, energy decline rate was influenced much less than the other measures by changes in vegetation density or other physical properties. This feature would therefore make it a reliable distance cue even under changing environmental conditions. Similarly, behavioral playback experiments with the wren *Troglodytes troglodytes* suggest that potential distance cues might lie in the changed durations of the energetic pauses of transmitted song (Holland et al. 2001a; Holland et al. 2001b). This in turn depends on the amount and relative time of arrival of reverberated energy at the receiving end.

Because signal degradation in general and reverberation in particular appears to provide cues to distance, it mediates information transfer at some level, with the transmitted information being the distance of the signaler. In cases where the sender benefits from being correctly localized its vocalizations should incorporate features that degrade predictably over distance and cannot be manipulated. Based on accumulated evidence from the field studies mentioned above, a reliable feature that increases with increasing distance and is not prone

to cheating (i.e. dishonest signaling) on the signaler's part thus is the level to which signals are reverberated.

Ranging is thought to be a two-step process that requires (1) the assessment of the degree of signal degradation and (2) a comparison with an internally stored reference song that properly reflects the non-degraded structure of the song at the source and allows the receiver to map perceived degradation levels against a likely distance. The importance and underlying mechanism of the latter step, however, are not yet clear (Morton 1982; Morton 1986; Wiley 1998; Brumm and Naguib 2009).

In this study the goal is to build upon the results obtained in Study I and investigate the birds' ability to categorize reverberation times across vocalizations, an ability that should be independent of prior experience with the stimuli at any reverberation level but may improve with familiarity. I again tested birds of three different species (budgerigars, canaries, and zebra finches), this time in a psychoacoustic categorization task that allowed for tests with less familiar, randomly presented probe stimuli that had to be assigned to previously learned reverberation categories. For this purpose, all reverberation-induced changes of the signals, including signal elongation due to tails of echoes, were preserved to assay the birds' ability to perform categorization tasks on the basis of non-manipulated acoustic features they would encounter under more natural circumstances. The focus therefore was on the synergistic effects of within-signal changes *and* elongation by echoes.

I expect the birds to be capable of learning different reverberation categories and subsequently assigning less known stimuli to these categories. This ability may be restricted to rather distinctive categories that differ greatly in their reverberation level. Moreover, given the generally superior auditory sensitivity of budgerigars and their life-long ability to learn large numbers of new vocalization compared to the other two tested species, I predict that budgerigars should be better at categorizing reverberation than canaries or zebra finches.

3.2.2 METHODS

Subjects

The test subjects were four adult budgerigars (2 males, 2 females), three canaries (males only), and four zebra finches (2 males, 2 females) that were all housed in individual cages in the same vivarium at the University of Maryland, College Park. They were housed together with multiple other individuals from the same three species at a constant light-dark cycle to avoid potential seasonal changes in hearing sensitivity. Zebra finches were offspring from birds obtained from commercial dealers, while budgies and canaries were purchased directly from dealers at less than about one year of age. Only birds with normal, species-typical audiograms and were selected for this study. All birds had been participants in previous reverberation experiments and therefore were experienced with a variety of reverberated sounds. The daily food consisted of standard parakeet, canary, and finch seed mixes and was fed at the end of the day and during the

weekend. Birds were reinforced with yellow millet during experimental sessions. The weight of the birds was monitored daily and kept between 85 and 90% of their free-feeding weight.

Apparatus and Psychophysical Task

Details regarding the psychophysical set-up and the equipment controlling all experimental events including stimulus playback are described in detail in Study I.

The bird were tested in a GO/NOGO Classification Task, in which either a GO or a NOGO stimulus is presented upon initiation of a trial and the bird is required to give (GO) or withhold (NOGO) a response. The GO and NOGO stimuli are comparable to respectively the target and background stimuli in an Alternating Sound Task, except that in the classification task, the GO stimulus is not compared to a continuously repeated background of the NOGO stimulus. Instead, GO and NOGO stimuli are presented separately and at random once the bird initiates a trial. Thus, in contrast to the Alternating Sound Task, a bird is required to hold the GO and NOGO stimuli in long-term memory and give or withhold a response depending on the presented stimulus.

Stimuli and Reverberation Categories

Baseline stimuli, with which birds were trained, consisted of 12 different types of short vocalization segments, four of each of the three species, which stemmed from our library of high-quality, digital recordings (Figure 1). The segments were all representative of the given species' vocalization and chosen to cover commonly

used song syllables, song phrases and calls. The baseline stimuli in the different sets were the same and differed only in their reverberation. For example, one set would consist of all 12 stimuli reverberated at one level, while the other set comprised stimuli reverberated at a different level. The duration of the stimuli varied and ranged from 125 to 1,050 ms to ensure that overall duration between degraded and non-degraded stimuli could not serve as a categorization cue. For example, a non-reverberated vocalization could be as long or longer in duration as the reverberated version of a different vocalization in the tested stimulus sets.

Three different vocalizations, one from each species, served as *probe stimuli*. Like the baseline stimuli, they were typical of the given species' vocalizations and ranged in duration from 425 to 900 ms (Figure 2). Each of the two sets of probe stimuli consisted of the three vocalizations that were reverberated at a particular level in one set and at another level in the other set, corresponding to the reverberation times of the two baseline stimulus sets.

All stimuli were artificially reverberated at 0, 50, 100, 300 and 600 ms using the same computer-implemented algorithm as described in Study I (see also Appendix II). Here, too, stimuli with reverberation times of 0 ms were used instead of non-reverberated stimuli. Contrary to the experimental approach in Study I, the goal of this study was to test the synergistic effects of within-signal changes *and* elongation by tails of echoes. I therefore preserved all echoes during signal processing. With a sound speed of about 340 m/s in dry air at 20°C, the reverberation times above correspond to the following additional travel distances

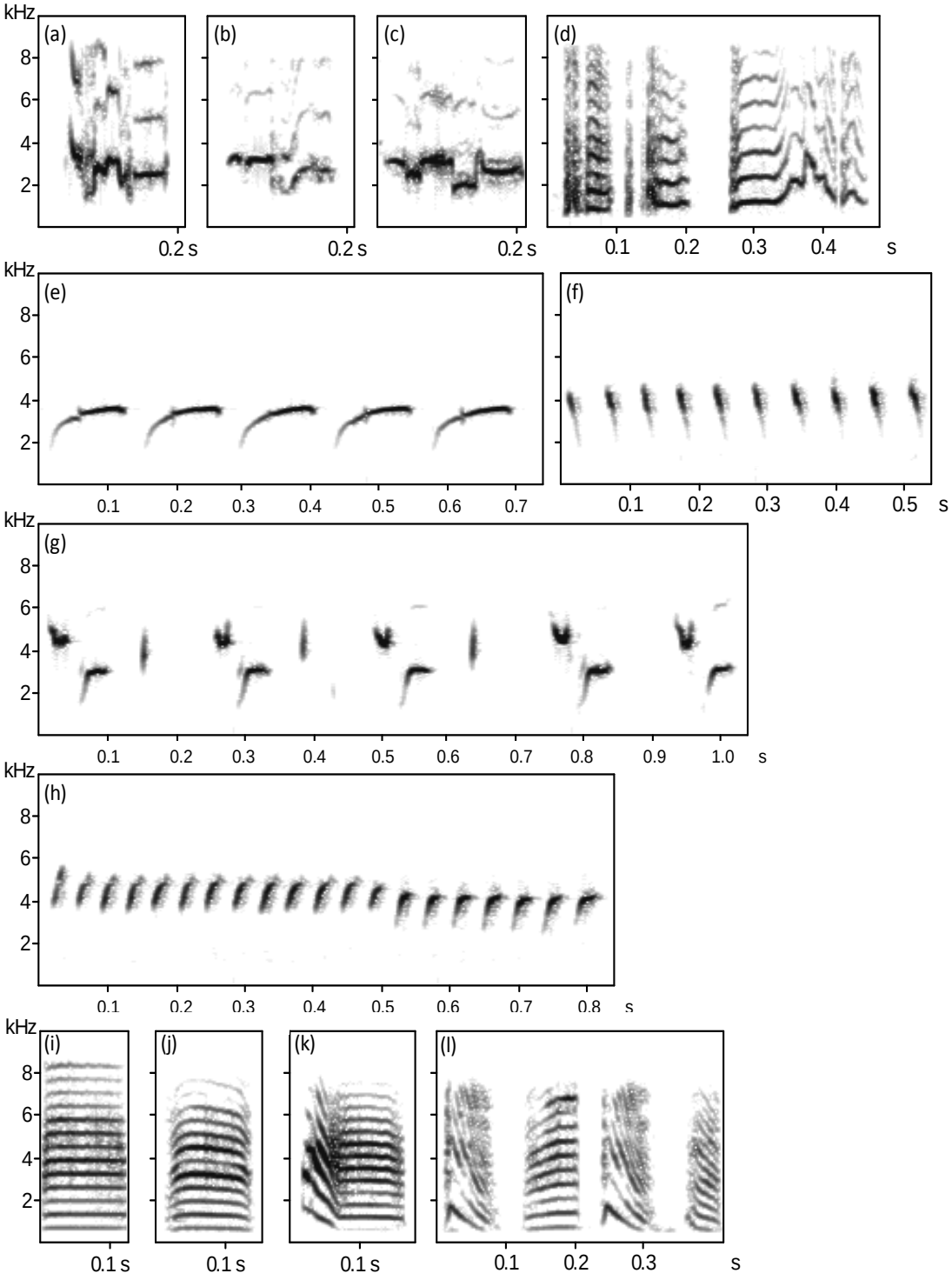


Figure 1. Spectrograms of baseline (i.e. trained) stimuli from three different species and of various durations. All vocalizations are taken from different individuals and comprise a mixture of calls, song syllables, and short song sequences. (a)-(d) budgerigar vocalizations; (e)-(h) canary vocalizations; (i)-(l) zebra finch vocalizations.

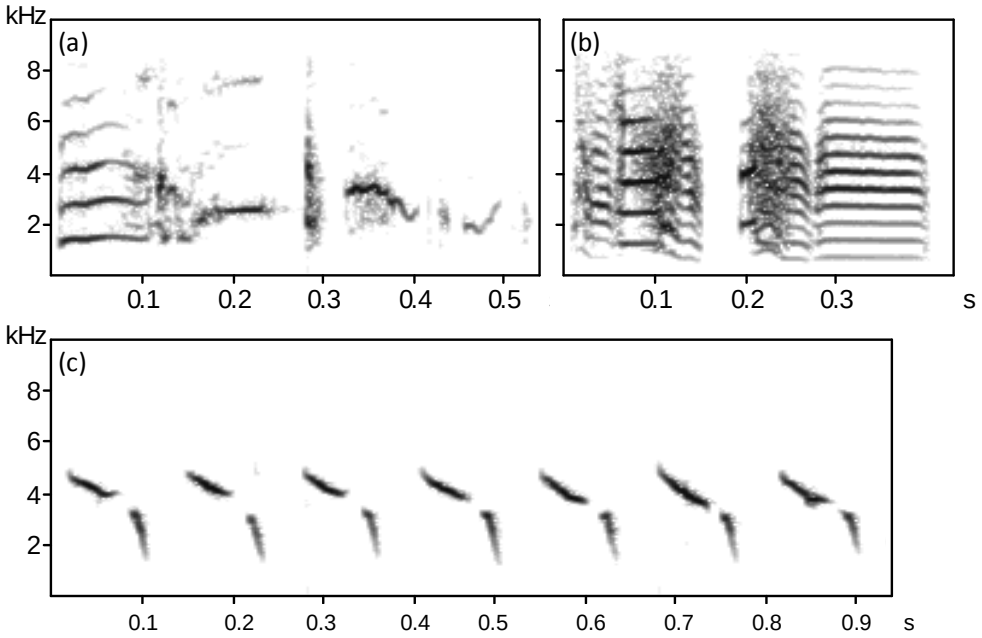


Figure 2. Spectrograms of probe stimuli from three different species and of various durations. All vocalizations are taken from different individuals. (a) budgerigar song sequence (warble), (b) two zebra finch syllables taken from a complete motif, and (c) canary song sequence.

of reflected sound waves relative to the direct path: 17 m (50 ms), 34 m (100 ms), 102 m (300 ms), and 204 m (600 ms). These are typical reverberation times found at a moderate communication distance between a sender and a receiver in various habitats. A reverberation time of 600 ms, for example, would be obtianed in a deciduous forest without leaves and at a communication distance of about 60 m (Blumenrath and Dabelsteen 2004). Six different category pairs were tested: 50 vs. 0 ms, 100 vs. 0 ms, 300 vs. 0 ms, 300 vs. 50 ms, 300 vs. 100 ms, and 600 vs. 300 ms.

Baseline Training

All birds had prior experience with operant conditioning methods and had been previously tested with reverberated stimuli. The training goal was that all test subjects be able to discriminate between two sets of baseline stimuli, each consisting of 12 segments of conspecific and heterospecific vocalizations. One set consisted of 12 stimuli with one particular reverberation time (GO stimuli), while the other set consisted of the same 12 stimuli at a different or no reverberation time (NOGO stimuli). At each trial only one stimulus was randomly picked from either of the two sets. The birds learned to give or withhold a response, depending on the category. To arrive at this goal, birds were trained stepwise by gradually adding more stimuli to each category until two complete sets could be discriminated correctly at least 80% of the time on average for two consecutive training sessions, which corresponds to a d' of 1.68 (performance criterion). Depending on the total number of GO and NOGO stimuli a training session lasted for at least 100 trials and up to a maximum of 240 trials, so that each stimulus was presented at least 10 times in each session. Training started with two stimuli in each set and with a 100% reinforcement or reward probability for correct responses to GO stimuli. Once the birds reached the average learning criterion of 80% correct responses (i.e. hits and correct rejections) to the stimuli from both categories for two consecutive sessions, two more stimuli were added to each set (i.e. a total of four new stimuli). This procedure was repeated four additional times until both sets were complete and all baseline stimuli were discriminated at

criterion level. In order for the birds to get used to only intermittent reinforcement, the reinforcement probability for correct responses to GO stimuli was gradually reduced to 80% over two or three sessions. This was supposed to prepare the birds for subsequent testing sessions with probe stimuli in trials that were neither rewarded nor punished and made up 20% of the total number of stimuli (see "Probe Sessions and Data Collection" below). Once the birds had completed a probe session, a new training phase with two new sets of reverberated baseline stimuli began.

Probe Sessions and Data Collection

In experimental test sessions the birds were also presented with stimuli that were more or less unknown to them in their reverberated form (so-called probe stimuli, see below). The birds initiated a trial by pecking the green observation LED. This was followed by the presentation of a randomly chosen stimulus from either of the two trained sets or, alternatively, from the new probe stimulus set. The delay between observation key peck and stimulus playback was fixed at 50 ms and playback only occurred once. The birds then had to either withhold or give a response within the allotted response time, the latter by pecking the red response LED. The start of the response interval was set to coincide with the onset of the sound and lasted for a total of 2.5 s.

A complete block of trials consisted of 30 trials. During 24 of these trials all 12 stimuli from each of the two baseline sets (GO and NOGO) were presented, while the remaining six trials were reserved for playback of the six probe stimuli

(three GO and three NOGO). All stimuli were drawn at random, with a maximum of three consecutive baseline stimuli of the same category occurring within one block. In other words, a maximum of six consecutive same-set stimuli could potentially be presented across blocks. I chose this maximum repetition rate to ensure that birds were not able to predict the category of subsequent stimuli, thereby reducing any tendency for guessing on the birds' part. Probe trials, on the other hand, were randomly inserted between baseline trials just one at a time. Only correct responses to baseline GO stimuli were reinforced with a 2-s access to seeds from the food hopper. With a reward probability of 100% for GO stimuli and six non-rewarded probe trials per 30-trial block, the overall reinforcement rate was 80%, i.e. the same rate, at which birds were reinforced during the final stages of baseline training.

All test birds had to complete 10 blocks (or a total of 300 trials) before they were moved on to a new training phase. Once the probe sessions were completed for a given category set or pairing, training was repeated for a new combination of categories. During test sessions, birds had to maintain consistent performance for baseline categories for all consecutive 300 trials, i.e. it had to be equal to their final performance during baseline training (see above). Otherwise birds were subjected to further training until performance was consistent. However, this was usually only necessary if test sessions were interrupted by longer breaks, such as weekends. As mentioned earlier, a total of six different category pairings were tested ((1) 300 vs. 600 ms, (2) 300 vs. 100 ms, (3) 300 vs. 50 ms, (4) 300 vs. 0 ms,

(5) 100 vs. 0 ms, and (6) 50 vs. 0 ms), and all subjects of each species were trained and tested with these categories in random order. This way, birds may or may not have previously experienced probe stimuli at a certain reverberation level, depending on the category pairs tested in preceding sessions. Compared to baseline stimuli, which birds were trained on for several thousand trials, prior experience with probe stimuli was next to negligible, given that each probe stimulus was presented only 10 times at a particular reverberation level during a complete test session.

Data from a total of 300 trials were used to obtain percentages for hits (correct positive response to GO stimuli), misses (withheld response to GO stimuli), correct rejections (correctly withheld response to NOGO stimuli), and false alarms (false positive response to NOGO stimuli). Response percentages for baseline stimulus sets and probe stimulus sets were obtained separately and each converted to the sensitivity index d' (for a "yes/no" task) to allow for valid performance comparisons across species and conditions. As described earlier, d' is based on relative z-scores for both hit and false alarm rates (see 2.2.5 "Measuring Auditory Sensitivities in the Lab," Appendix I, or Macmillan and Creelman 2005 for more details). Due to the perceptually more challenging tasks in this experiment of having to hold perceptual categories in long-term memory rather than making immediate comparisons between stimuli, I tracked discrimination sensitivities (expressed as d') against a performance level of d' = 1.0. This can still be considered a moderate performance for discriminating and assigning stimuli to

their proper reverberation categories. It corresponds to hit and false alarm percentages of e.g. (HIT/FA) = (50/16) (see table in 2.2.5 “Measuring Auditory Sensitivities in the Lab”).

Statistics

Statistical analyses were performed in SPSS (PASW Statistics 18, 2009). I conducted a univariate Repeated Measures Analysis of Variance with one between-subject factor (species) and one repeated measures factor (reverberation category pair). Two dependent variables, d’ (baseline) and d’ (probes), were included in the ANOVA but analyzed separately. Species served as the independent, i.e. between-subjects factor, which divided all subjects into groups. (For details on repeated measures ANOVA designs with one between-subjects factor refer to Hand and Taylor 1987.) I tested homoscedasticity by using Levene’s Test of Equality of Error Variances for the between-subjects factor and Mauchly’s Test of Sphericity for within-subjects factors. I additionally inspected spread-versus-level plots that graph standard deviations against factor level means. The data fulfilled assumptions of sphericity, normal distribution and equal variances across factor levels. To reveal potentially significant differences between levels of all factors Bonferroni-adjusted multiple comparisons were performed

To test for statistically significant differences between the two variables d’ (baseline) and d’ (probe), I performed a Paired Sample T-test (two-tailed). The results of this test allowed me to assess whether the introduction of probe stimuli changed the subjects’ performance and to what extent. If

performance were to significantly decrease for probes, this could suggest that members of a category need to be memorized and new stimuli cannot be reliably assigned to it. The t-test also produced the Pearson correlation between the variable pairs, which indicated the strength and direction of their association, as well as 95% confidence intervals for the average differences.

3.2.3 RESULTS

During baseline training, all birds achieved discrimination well above d' = 1.0 between categories, even when reverberation differences were rather small (e.g. 50 vs. 0 ms). They performed considerably worse, however, when both sets contained highly reverberated stimuli, even if the actual reverberation difference was large (Figure 3 (a)). For instance, 600 vs. 300 ms posed more problems than 300 vs. 0 ms and in fact yielded the overall lowest average d' (1.53), despite the same relative reverberation difference. Sensitivity indices for baseline (i.e. trained) stimuli ranged on average from 1.53 (600 vs. 300 ms) to 3.06 (300 vs. 0 ms), whereas those for probe stimuli ranged from 1.04 (600 vs. 300 ms) to 2.39 (300 vs. 0 ms).

Across all samples, d' significantly dropped from 2.14 to 1.52 on average when birds were tested with probe stimuli (two-tailed T-test: $t = 11.411$, $df = 65$, $P < 0.001$; Figure 3 (c)). Although this drop in performance was significant, the average d' for probe stimuli remained above 1.0, which corresponds to a moderate sensitivity toward sound differences (see 2.2.5 "Measuring Auditory

Sensitivities in the Lab"). There was also a significant positive linear correlation between the variables (Pearson two-tailed test: $r = 0.869$, $P < 0.001$, $N = 66$). The relationship between the two variables is illustrated in Figure 3 (d) and clearly shows that d' (probe) is consistently lower than d' (baseline).

The repeated measures analysis of variance revealed a significant effect of the between-subjects factor Species and the within-subjects factor Reverberation Category Pair on both dependent variables, whereas their interaction was non-significant (Table 1). Although the within-subjects factor had a more significant

Table 1. Repeated Measures ANOVA table showing results for between- and within-subjects effects and their interactions ($\alpha = 0.05$). Univariate test results are displayed to show effect differences between baseline and probe stimuli. The model uses Type IV Sums of Squares for unbalanced designs. Each factor has similarly strong effects on performance with baseline and probe stimuli. Factors with the strongest significant effects are reverberation category and species.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Between-Subjects*					
Species					
- baseline	2	1.311	0.656	5.810	0.028
- probe	2	0.819	0.409	4.962	0.040
(2) *Within-Subjects*					
Reverberation Category Pair					
- baseline	5	18.295	3.659	10.311	<0.001
- probe	5	13.917	2.783	8.413	<0.001
(2) *Interactions*					
Species x Reverberation Category Pair	10	4.861	0.486	1.370	0.229
- baseline	10	4.191	0.419	1.267	0.241
- probe					

effect on either variable than Species, the latter contributed slightly more to the overall data variation than the former (Species: $\eta^2 = 0.592$ (baseline), $\eta^2 = 0.554$ (probe); Reverberation Category Pair: $\eta^2 = 0.563$ (baseline), $\eta^2 = 0.513$ (probe)).

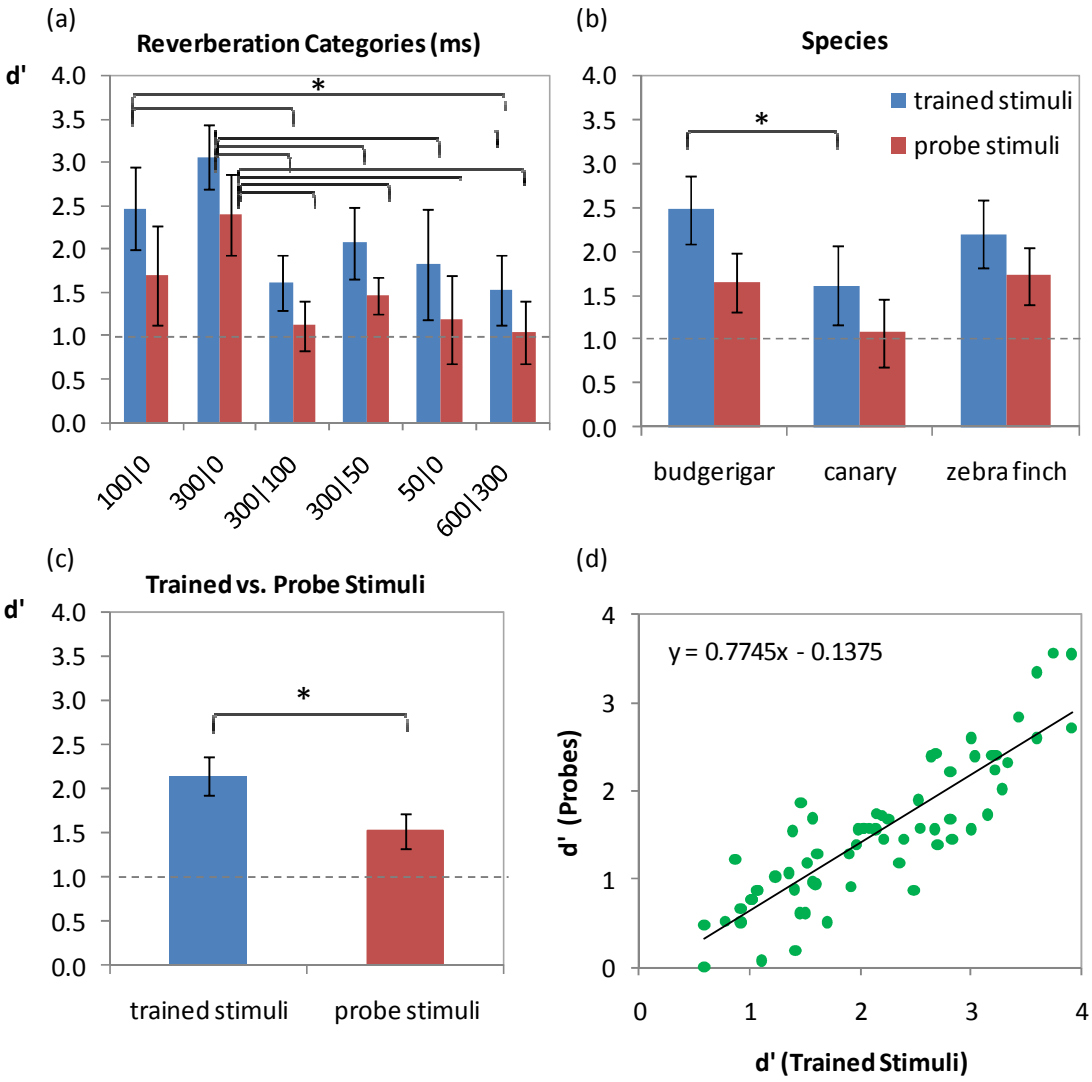


Figure 3. Significant main effects showing 95% Bonferroni-adjusted confidence intervals around estimated marginal means (a)-(c). Average performance with probe stimuli was consistently lower for all species but remained well above or just around a d' of 1.0 (b)+(c) even across tested category pairs (a). Budgerigars performed best, and some categories were easier than others (e.g. 100|0 and 300|0 ms) even when the relative reverberation difference was the same (e.g. d'(600|300) < d'(300|0)). The overall relation between the response sensitivities toward probes and baseline (or "trained") stimuli is shown in (d), indicating a strong positive correlation (r = 0.869, see text). Significant differences between factor levels are marked with *****. The stippled lines equal a discrimination sensitivity of d' = 1.0.

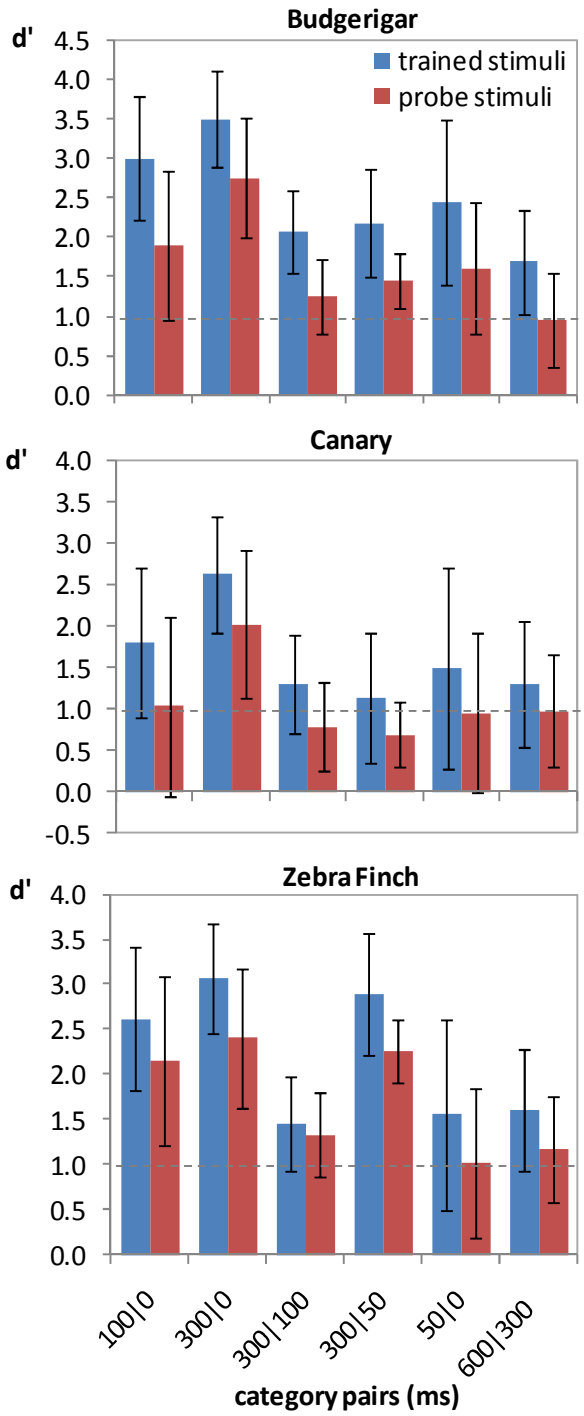


Figure 4. Response sensitivities shown for all three species separately. Each graph compares results for both trained and probe stimuli within each reverberation category pair. 100|0 and 300|0 ms category pairings were among the easiest for all species. The three species showed similar performance patterns across categories, except 300|50 ms. The stippled lines mark a discrimination sensitivity of d' = 1.0. Bars represent Bonferroni-adjusted 95% CIs around estimated marginal means. Only non-overlapping bars are indicative of significant differences.

Budgerigars and zebra finches performed about equally well, but only budgerigars were significantly better than canaries (Figure 3 (b)) at assigning stimuli to their proper categories and only when the stimuli were those they were previously trained on (baseline stimuli). Figure 4 shows the response sensitivities for the three species separately. All species had a comparatively greater sensitivity toward discriminating stimuli when the tested category pairings were either 100 vs. 0 ms or 300 vs. 0 ms reverberation time. With regard to the remaining categories, there was less consistency among species, and their sensitivities varied greatly. For example, while 300 vs. 50 ms was a relatively easy category pair for zebra finches, it was the most difficult one for canaries (Figure 4). Despite the differences, the interaction effect was non-significant (Table 1).

3.2.4 DISCUSSION

The main objective of this study was to establish the ability of three species of birds to categorize various reverberation times across conspecific and heterospecific vocalizations and to test the extent to which familiarity with the stimuli at the tested reverberation times plays a role in this ability. Overall, the results suggest that levels of reverberation can be categorized across different types of vocalization both for new and learned stimuli. It is clear, however, that some categories are more easily distinguished than others – particular those that reflect distance differences at relatively short range. Even though it may at first

seem counterintuitive that smaller differences between categories of low reverberation times are more readily distinguished than large differences at high levels, it would nonetheless be plausible if accurate assessment is more important in relatively short-range interactions compared to judging the whereabouts of a far-away individual. This is particularly true in the context of resource defense, where very distant individuals far away from important resources or outside territory boundaries are not a particular threat while close ones may be, especially if they are intruding on a territory or approaching nesting sites and areas with important food sources. Usurpers like these require immediate action, and the ability to localize them accurately helps direct quick and appropriate behavioral responses toward the target individual without wasteful searches.

The results also indicated that extensive prior knowledge of the sounds at the tested reverberation times is important but not entirely necessary for correct categorization. Stimuli that have not or only occasionally been encountered at these levels can still be correctly assigned to the proper category, albeit with significantly less acuity. Greater familiarity with the reverberated forms of a vocalization therefore does seem to help considerably. This discrepancy between vocalizations with highly familiar and less or unfamiliar reverberated versions could potentially be reflective of typical listening contexts in natural environments. In many situations the most frequently encountered and biologically important distances are between the listener and a known signaler, such as a neighbor, a flock member or kin. In established groups or networks like

these, proper assessment of such individuals is pivotal and can potentially save energy by avoiding costly interactions. For instance, if a neighbor is at its expected location, no territorial disputes are necessary. Similarly, if mates, kin, or flock members are out of sight but their distance can be assessed correctly, there is more certainty as to their whereabouts so that direct approaches are facilitated and mistakes prevented. Retaining this ability also for less known signals is nonetheless important for both males and females in encounters with individuals that are less frequently heard. The latter would have, e.g., more distant territories or live in different flocks. In territorial species, occasional interactions may have occurred during initial territory establishment or mate attraction and selection earlier in the season or during feeding in winter flocks. In flock species, on the other hand, other groups may on occasion come close enough to be audible, especially if nomadic species seek out places of similarly high resource quality. In either case, situations can arise in which interactions with these less familiar birds are likely and correct estimation as to their location is beneficial.

Overall, the reported improvement of categorization abilities with increased familiarity with the reverberated sounds is not entirely surprising. In humans, too, accurate distance estimation of a sound source is considerably influenced not only by the type of signal (Shinn-Cunningham 2000) but also the listener's experience with the tested sound and the acoustic environment. Experienced subjects can detect changes in distance between sound source as little as 5% (Strybel and Perrott 1984), and visual cues considerably increase

accuracy (e.g. Mershon et al. 1981; Min and Mershon 2005). Field experiments with birds have also shown that the perceived distance of novel sounds are invariably underestimated (McGregor et al. 1985; Little et al. 1992). Furthermore, distance perception in natural contexts can change if there is a certain expectation as to the location of a sound source (Mershon et al. 1980; Min and Mershon 2005), and as discussed in Study I, noise can considerably change the percept of reverberation. Yet, utilizing multiple cues as seen in humans and in visual communication (Mershon and King 1975; Davies and Green 1994a; Davies and Green 1994b) as well as determining signal direction can considerably aid correct source localization, independent of signal familiarity (Naguib and Wiley 2001a).

The three tested species differed in their ability to categorize stimuli according to their reverberation level. As predicted, budgerigars were generally better at this task while canaries were worst, but this difference was significant only for baseline stimuli. Figure 4 shows, however, that zebra finches are the only species whose performance with either baseline or probe stimuli never reached levels below relative moderate levels equivalent to a d' of 1.0 (see 2.2.5 "Measuring Auditory Sensitivities in the Lab"). It is clear that canaries had the greatest difficulty, especially with vocalizations whose reverberated forms were not known (probes). In this case, the majority of category pairs posed such great difficulty for canaries that the birds were unable to reliably categorize the reverberation level of these stimuli, and their performance was mostly just below a d' of 1.0. The general superiority of budgerigars is hardly surprising given their

ability to learn large numbers of new vocalizations throughout life and to retain vast amount of these in their active repertoire.

Sound source localization under natural conditions poses a great challenge to the integrative abilities of the auditory system, since the precise localization of a source is a result of the combined evaluation of many available pieces of information on its distance and direction, such as within-signal cues (due to propagation through the environment), binaural cues (from the direction and elevation of a source), and cues from the position of reflective surfaces (the so-called precedence effect) (Zurek 1980; Klump et al. 1986; Mershon et al. 1989; Carr and Konishi 1990; Middlebrooks and Green 1991; Little et al. 1992; Hartmann 1997; Huang et al. 1997; Naguib 1997; Nelson and Stoddard 1998; Litovsky et al. 1999; Nelson 2000; Macpherson and Middlebrooks 2002; Konishi 2003). Of course, the full complexity of this task cannot and should not be replicated in the lab if the aim is to understand the relative usefulness of each of these pieces of information. My experiments essentially simulated five different distances in the form of reverberation times in a non-specified reverberant environment, and the equalized overall sound level ensured that reverberation was the only cue available. If the characteristics of a particular environment and the used signals are known it is possible to translate these findings into actual signaler-receiver distances in selected habitats. While I demonstrated that small bird species, especially budgerigars and zebra finches, can distinguish between most of the tested categories based on reverberation times alone, it is still unclear whether

birds could use reverberation as an absolute or a relative cue. This can only be tested in phonotaxis experiments similar to those that have been conducted in studies investigating other cues to distance in the field (e.g. Naguib 1995, 1996b; Nelson and Stoddard 1998; Holland et al. 2001a; Mason et al. 2005; Bernal et al. 2006). In sound localization in humans, reverberation is known to serve both as a relative and an absolute cue (von Békésy 1960; Mershon and King 1975; Mershon and Bowers 1979; Mershon et al. 1989). For instance, human listeners always estimate reverberated sounds or sounds in a reverberant environment as being farther away than non-reverberated sounds or sounds in anechoic chambers (Mershon and King 1975). There is some indication in my findings as to the nature of the reverberation cue. If birds were to use it as a relative cue, same relative differences between reverberation times at both high and low overall levels across sounds should be equally distinguishable. Yet, my experiment has revealed that sounds whose reverberation times differ by, e.g., 300 ms (which is equal to an additional path length for reflected waves of about 100 m) are significantly less accurately categorized when their absolute reverberation times are 300 and 600 ms compared to 0 and 300 ms (Figure 3 (a)). Instead, this finding suggests that reverberation could be used as an absolute cue at relatively short range.

Future experiments should also investigate the influence of background noise on perceived distance in reverberant habitats. In humans, the presence of noise has been demonstrated to make stimuli sound much closer than they actually are (Mershon et al. 1989). This is because noise masks the weaker,

reflected sound waves relatively more than the much louder, direct waves, thereby reducing the percept of echoes, whose duration and amplitude are important distance cues also in birds (e.g. Naguib 1995; Holland et al. 2001a). To test the same phenomenon in birds, the present experimental design could be modified to contain probes that have varying levels of underlying background noise, whereas the baseline stimuli of each category remain noise-free.

Methodological Considerations and Suggested Improvements

An alternative to the present design, which requires a withheld response to a NOGO baseline or probe stimulus, would be a paradigm in which each category is assigned to a separate response key[*]. A withheld response would then clearly indicate uncertainty about the correct category assignment of a presented sound. This paradigm in turn can be criticized for promoting guessing that is comparatively harder to detect. It would also have necessitated changes of the available psychophysical apparatus as well as the program that controls the experimental events via TDT System III (see "Methods"). At this point, there is no single correct way of testing stimulus categorization in animals. But this should not prevent researches of animal sensory systems from addressing important questions in the perceptual realm of categorization, as long as there is awareness about the shortcomings of each of the possible procedures and conclusions are drawn with caution.

[*] In the bird literature this procedure is confusingly called the Two-Alternative-Forced-Choice (or 2AFC) procedure (e.g. Klump 1996), which differs from the 2AFC paradigms commonly used in human studies (e.g. Macmillan and Creelman 1991, 2005).

Another consideration to be made is that, traditionally, probe stimuli often are sounds with features that fall somewhere in between the two test categories. I made the conscious choice of only using stimuli that had either one or the other feature (i.e. no intermediate states), because my research question was formulated in such a way that the goal was to see whether birds can learn stimulus categories and assign less familiar stimuli to them and not what the category boundaries are. This would be a separate research question in itself that should be addressed in future studies. Moreover, although such a question is relevant, I do not find the methodological approaches available for animal studies today reliable enough to be confident about the results. Regarding the choice of stimuli overall, some baseline stimuli were harder to discriminate than others. I should point out, therefore, that the objective was not to investigate stimulus design as a factor. Furthermore, the differences did not seem to follow any discernible pattern. However, since there is evidence from human studies that the accuracy of distance estimation is dependent on the properties of the signal (e.g. Strybel and Perrot 1984), it would be worth testing stimuli on the basis of particular design features that can be isolated and individually controlled. Specific features that promote categorization of reverberation times should be useful in distance estimation and therefore ought to be utilized by those bird species that benefit from accurate source localization. Inspiration for such experiments could be found particularly in the various signals used by echolocating bird and mammal

species who successfully exploit the reverberation characteristics of the acoustic signals used in echolocation and the surrounding environment.

Instead of testing categorization based on composite cues of reverberation (i.e. both signal distortions and elongations) one could test categorization of the same stimuli either without echoes or without distortions within the signal to isolate each of these cues and assess their usefulness independently. Here, the goal was to mimic more realistic conditions under which stimuli normally would have to be grouped into categories. This seemed a reasonable first step in terms of the research question at hand and with the initial uncertainty whether birds could in fact be successfully trained to categorize reverberation. Testing the birds under the easiest possible circumstances first, therefore, appeared to be a sensible initial approach.

3.3 Study III

Effects of Reverberation on the Discrimination of Similar but Individually Distinct Vocalizations

3.3.1 INTRODUCTION

Vocal communication among small birds often involves a variety of vocalizations such as calls and songs, which in turn vary within and across individuals. Typically, singing individuals have a repertoire of several different song and call variations, some of which can be very similar to those produced by other individuals in the same social network (Catchpole and Slater 1995). In acoustic signals like these, information regarding species and individual identity is encoded in the acoustic properties of the emitted sound wave and in its temporal pattern of delivery (Dhondt and Lambrechts 1991; Lambrechts and Dhondt 1995; Bradbury and Vehrencamp 1998). A vocal signal can thus be uniquely characterized by its amplitude and frequency spectrum, duration, modulations of frequency and amplitude over time as well as its duty cycle. However, vocalizations are never produced under completely anechoic and quiet conditions. Habitat-induced reverberation can modify these characteristics and may ultimately obliterate parts of the encoded information and decrease its transmission range (Slabbekoorn 2004; Dabelsteen 2005). Reverberations alone have a tendency to modify the signal structure and ultimately remove some of the encoded information, whereas ambient or transient noise merely masks it (Houtgast and Steeneken 1973; Brumm and Slabbekoorn 2005). Together, both are responsible for joint spectro-

temporal distortions of the signals, with ambient noise contributing to the spectral dimension and reverberation giving rise to the temporal dimension of the observed alterations. Therefore, the extent of these modifications greatly depends on the signal structure, the physical characteristics of the habitat (Marten and Marler 1977; Wiley and Richards 1982; Bradbury and Vehrencamp 1998) as well as behavioral responses to these deleterious effects by signalers and receivers to compensate for decreased signal quality (Dabelsteen et al. 1993; Holland et al. 1998; Balsby et al. 2003; Blumenrath et al. 2004; Blumenrath and Dabelsteen 2004; Mathevon et al. 2005).

In songbirds, vocally mediated discrimination between conspecific individuals within a communication network is well-documented and forms the foundation of many social and reproductive behaviors. It serves the survival of the individual and, ultimately, the conservation of its species. A behavioral field study with female great tits revealed the ability of females to recognize their mate despite high song similarity and deteriorating acoustic conditions (Blumenrath et al. 2007). This is even more intriguing given that preliminary results with the songs of the same species have indicated that similar song types that are shared by neighbors become yet more similar in structure when they are subject to habitat-induced degradation (Blumenrath 2003). Spectrum differences and differences in amplitude and frequency patterns over time seemed reduced and duration more equalized across song types, which could interfere with individual recognition. Evidence from psychoacoustic studies with humans, too, suggests that speech

degradation, brought about by artificially and naturally created room reverberations of variable decay times, results in deterioration of speech segments and, consequently, speech intelligibility (Harris and Reitz 1985; Harris and Swenson 1990; Helfer and Wilber 1990; Gordon-Salant and Fitzgibbons 1995a, b; Fitzgibbons and Gordon-Salant 1996). Studies with normal hearing humans and elderly listeners in particular have shown that temporal degradation caused by reverberation can have immense impacts on the perception of speech or single consonants, and that the simultaneous presence of noise compounds these detrimental effects (e.g. Harris and Reitz 1985; Harris and Swenson 1990; Helfer and Wilber 1990; Gordon-Salant and Fitzgibbons 1995a).

Despite ample human research in this field, studies with animals are so far rare. This study investigates the combined reverberation and noise effects on the perception of similar but individually distinct vocalization that differ only subtly in temporal and spectral patterns, such as AM, FM, rhythm, duration or overall spectral shape of the sounds. It focuses on three species of small birds (the budgerigar, canary and zebra finch) and their species-typical vocalizations. The combined effect of reverberation and background noise is an attempt to mimic the acoustic conditions of noisy, reverberant environments.

Zebra finches are 'closed-ended' learners, who learn their songs mainly from their father but also from other individuals in their surroundings during the sensitive learning period shortly after birth, after which their repertoire is relatively fixed. Canaries and budgerigars, on the other hand, are 'seasonal' and

'open-ended' learners, respectively, who are able to learn and imitate new vocalizations throughout their lives and do not have designated song tutors. All three of these species show vocalizations that can be highly similar to the vocalizations of individuals nearby. It is thought that every auditory system has species-specific mechanisms that make it especially sensitive to the respective species' own vocalizations and changes therein (Dooling et al. 1992; Bass et al. 1999; Hauser and Konishi 2003; Brumm and Naguib 2009).

Subjects of all three species were trained in an Alternating Sound Task using operant conditioning methods to discriminate between pairs of non-reverberated vocalizations of two different conspecific or heterospecific individuals. Distinctions had to be made between the repeating background of one individual's vocalization (A) and a randomly inserted similar vocalization from a different individual (B). Birds were then tested with different vocalization types of each species (calls, syllables, and short song sequences) at various reverberation times with and without simultaneous noise. One prediction is that birds will simply memorize or habituate to the continuous background of individual A's reverberated vocalization, which would allow for easy discrimination of a sufficiently different target stimulus independent of its reverberation. If discrimination does depend on reverberation times, however, it could suggest that a mechanism other than memorization is the cause for their performance, and that birds may learn to recognize common features and the overall similarity of individual A's reverberated vocalization. As a result, similar but distinguishable

vocalizations from both individuals may be perceived as more similar in their reverberated form due to a 'smearing' of fine structural details in the temporal domain, masking of adjacent syllables from echoes, smoothing of the temporal envelope, and overall duration changes. All of these effects potentially render sound duration cues as well as subtle spectral and amplitude patterns within vocalizations less reliable. In addition, discrimination can be expected to be further complicated when sounds are discriminated under noisy conditions.

Reverberation and noise effects on discrimination are important in species that exhibit song sharing or other forms of vocal imitation and can bear important implications in communication networks for social behaviors that are mediated by individual recognition. However, because of the high fitness costs associated with discrimination errors in species that use songs in mating contexts, territorial defense and/or parent-offspring interactions, they should somewhat preserve their ability to distinguish vocalizations from different individuals also under sound-degrading conditions.

3.3.2 METHODS

Subjects

In this experiment, I used one male and two female adult budgerigars (*Melopsittacus undulates*), one male and two female adult zebra finches (*Taeniopygia guttata*), and three male adult canaries (*Serinus canarius*). The auditory sensitivity of female canaries varies with season, and although the animal

rooms, in which all birds were housed, were on a constant light-dark cycle to control for seasonal light effects, the best way to avoid any unwanted effects was to only test males. The birds were housed in separate cages in the same room with controlled access to food and water. All birds had previously been trained and tested in operant conditioning tasks and had participated in some or all previous studies presented in this dissertation. They therefore had prior experience with a large variety of reverberation times in this type of experimental setting. (See Study I and II for more details.)

Sound and Noise Stimuli

Stimulus sets consisted of two similar segments of natural vocalizations (referred to from now on as 'stimulus pairs'), one of each of two individuals of the same species, that were unfamiliar to the test subjects. Three different types of stimulus pairs of each of the three tested species were used, yielding a total of nine different pairs. The three types of vocalizations included single contact calls, short segments of songs, and single song syllables that were taken from recordings made with a Marantz PMD670 digital recorder at a sampling frequency of 48,000 Hz (16 bit). Figure 1 lists three examples of stimulus pairs used in the experiment (refer to Appendix V for the complete set of non-reverberated stimulus pairs). Test stimuli were played back at a level of 70dB SPL (A, fast setting) via TDT (Tucker Davis Technologies, Gainsville, FL) System III modules (see Study I) with an additional roving of ±3 dB to avoid slight differences in perceived loudness to serve as a cue in discrimination. Similarity was determined acoustically and

visually by inspecting spectrograms and oscillograms. Total duration of all stimuli and overall temporal patterns of song or warble sequences were similar within each pair to prevent birds from using large temporal differences as a cue to individual identity, while some temporal variation was desirable in answering the research questions addressed in this study (see 3.3.1 "Introduction"). A 2-min sequence of band-limited white noise was generated in Matlab 7.5.0 (R2007b, The Mathworks Inc. 2007) with low and high band limits at 0.5 and 8.0 kHz, respectively. It was presented as a continuous loop of noise at 60 and 70 dB SPL (A, fast setting) via TDT System III (see above), which is equivalent to a spectrum level (per cycle energy distribution, dB/Hz) of 21.3 and 31.3 dB[‡‡].

All stimuli were artificially reverberated at 0, 10, 50, 100, 200, 300, 400, and 500 ms using the same computer-implemented algorithm as described in Study I (see also Appendix II). Single elongations due to tails of echoes were preserved (Figure 2). Here, too, stimuli with reverberation times of 0 ms were used as a non-reverberated or control stimuli to evaluate the impact of signal distortion and elongating echoes on the perceived similarity of these sounds.

[‡‡] Spectrum level is calculated by first converting the measured noise SPL into pressure P (in Pa): $20\,log\,P\ = noise\ SPL$ (solve for P). Spectrum level is then equal to 10 log $\frac{P^2}{bandwidth}$, with bandwidth = width of noise band.

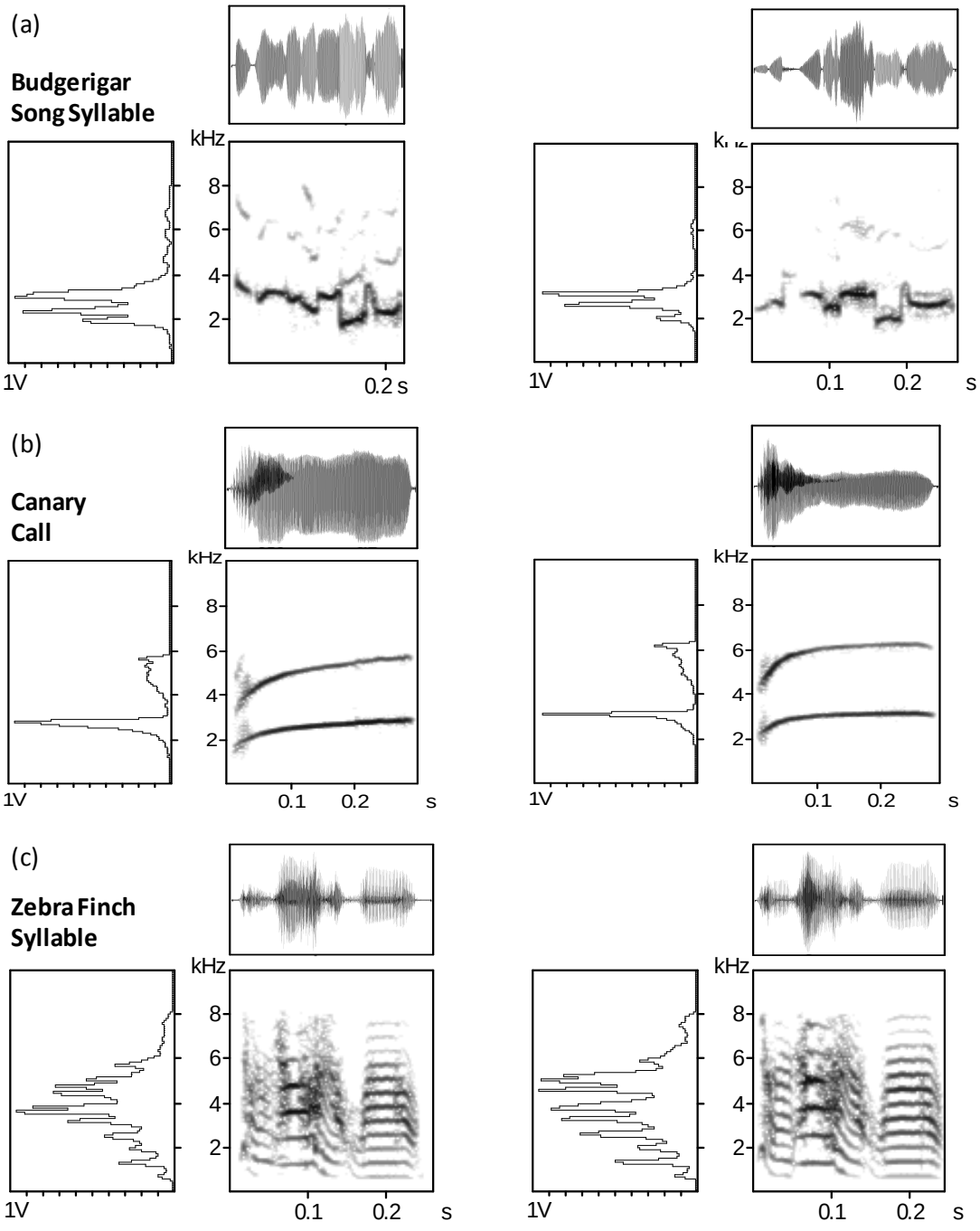


Figure 1. Three examples of non-reverberated pairs of similar stimuli from different individuals: (a) budgerigar syllables, (b) canary contact calls, (c) zebra finch syllables. Stimuli of a pair are positioned next to each other. Syllables are taken from complete songs or warbles. Spectrogram (middle), oscillogram (top), and frequency spectrum (in V) (left) are sown for each vocalization. The spectrogram has frequency (in kHz) on the y- and time (in s) on the x-axis.

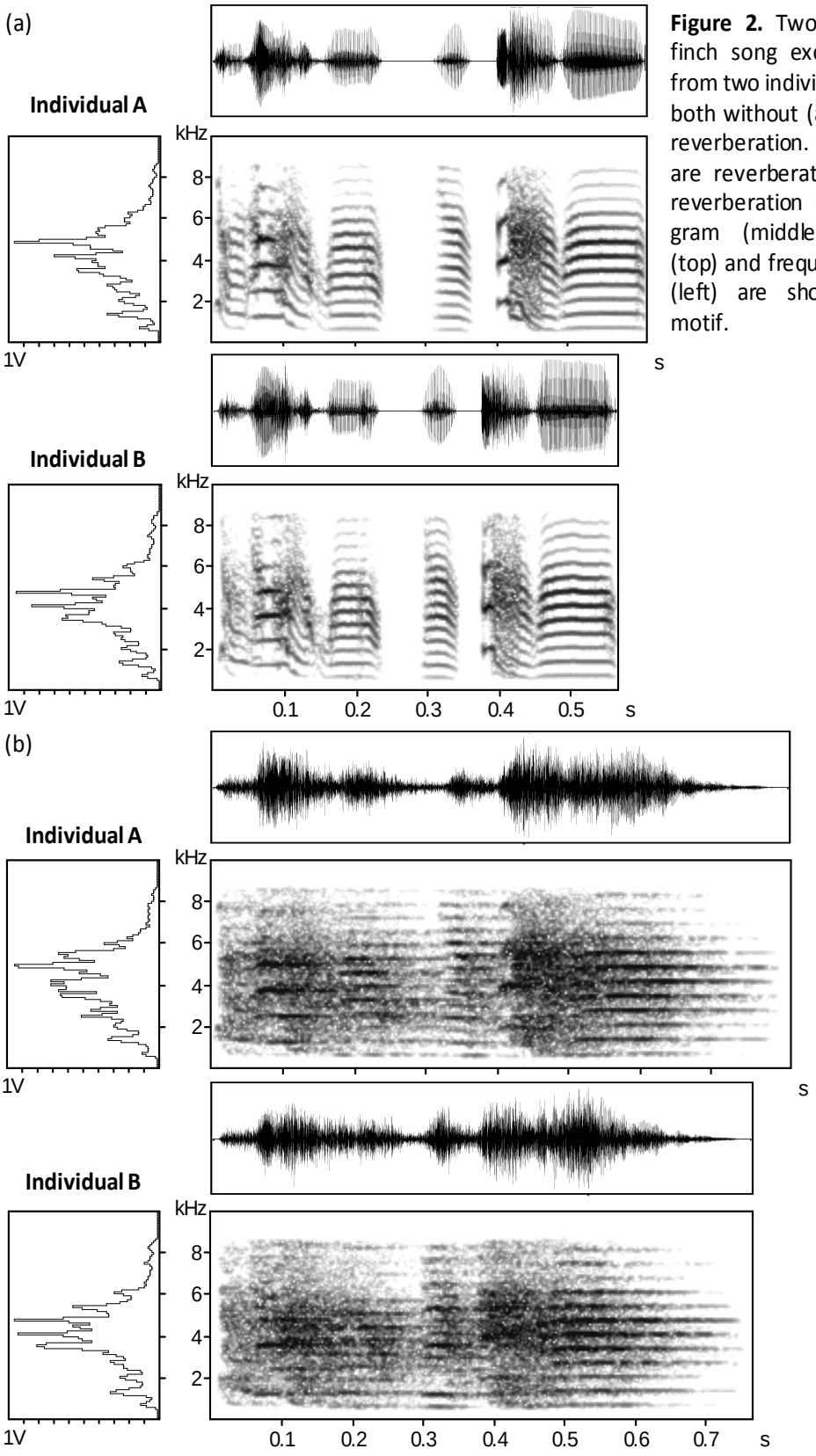


Figure 2. Two similar zebra finch song excerpts (motifs) from two individuals (A and B) both without (a) and with (b) reverberation. In (b) motifs are reverberated at 200 ms reverberation time. Spectrogram (middle), oscillogram (top) and frequency spectrum (left) are shown for each motif.

Psychophysical Task – Training and Testing Procedure

The general training and testing procedure are described in detail elsewhere (Park et al. 1985; Dooling and Okanoya 1995). The method of Constant Stimuli was used to test the subjects in an Alternating Sound Task, in which the subjects had to detect a change in a continuously repeated background sound (see Study I and Gulick et al. 1989; Dooling and Okanoya 1995).

Birds were trained to discriminate between the non-reverberated sounds of each pair (i.e. the background and target stimulus) with hits and false alarms of ≥ 95% and ≤ 10%, respectively, which corresponds to a d' of about 3.0 or higher. Once they achieved this for 200 trials in a row, two reverberated versions of the background stimulus were added, while the only target stimulus was still non-reverberated. Again, birds had to reach and maintain criterion performance for at least 200 successive trials before two more reverberated versions of individual B's vocalization (background) were added for further training. This procedure was repeated until the birds had learned to discriminate the non-reverberated target stimulus from the complete set of reverberated background stimuli at criterion performance level for at least 200 consecutive trials before they could proceed to actual test sessions with reverberated target stimuli. Birds were very quick to learn this task and could easily maintain consistently high performance levels for non-reverberated target stimuli.

A test session consisted of 10 blocks of 10 trials (i.e. a total of 100 trials), in which birds had to discriminate between two sets of stimuli (set A and B). Each

block contained eight trials with target stimuli (set A) and two sham trials (20%). The target stimuli were the single vocalization of individual A at eight different reverberation times (0, 10, 50, 100, 200, 300, 400, and 500 ms). As the repeated background (set B), individual B's corresponding vocalization was played back randomly and at fixed intervals at the same eight reverberation times (Table 1 exemplifies typical A and B stimulus sets). During playback the repeating background and alternating target stimuli were each randomly drawn from their respective sets. During the two sham trials in each block, a randomly chosen background stimulus from set B was presented instead of a target stimulus from set A.

CONDITION: ZEBRA FINCH CALL – NO NOISE

SET A – TARGET STIMULI	**SET B – BACKGROUND STIMULI**
Individual A	***Individual B***
1. 0 ms	1. 0 ms
2. 10 ms	2. 10 ms
3. 50 ms	3. 50 ms
4. 100 ms	4. 100 ms
5. 200 ms	5. 200 ms
6. 300 ms	6. 300 ms
7. 400 ms	7. 400 ms
8. 500 ms	8. 500 ms

Table 1. Example of a stimulus pair condition (similar zebra finch call from individual A and B at no noise). Set A and B each contain the respective birds' call (bird A or B) at eight reverberation times. During experimental session, the background stimuli were randomly drawn and played back repeatedly at fixed intervals. Once the bird initiated a trial, either a randomly chosen target stimulus or another background stimulus (sham trial) was alternated with the repeating background 2-6 s after trial initiation. Once a session was complete, the bird was transferred to a new experimental condition (e.g. "zebra finch call – with 60 dB noise "or "budgerigar syllable – without noise", etc.).

Test sessions continued as long as performance for the non-reverberated target stimulus in each session remained stable. Altogether the first two successive sessions or a total of 200 trials with consistent performance were included in the dataset. I tested the birds twice a day until they had completed all 27 conditions ($9_{\text{vocalization types}}$ x $3_{\text{noise levels}}$). Each bird was tested with different noise levels (0, 60 or 70 dB SPL) in random order. Performance was recorded as % correct responses to target stimuli (HITS) and % false alarms to shams or background stimuli (FA) and subsequently converted to the sensitivity measure d' to allow for unbiased comparisons of discrimination abilities across species and conditions. (Refer to 2.2.5 "Measuring Auditory Sensitivities in the Lab" and Appendix I for more details on the usage and computation of d'.). Performances were compared against a moderate sensitivity value of d' = 2.0, which correspond to hit and false alarm rates of e.g. 50% (hits) and 2% (false alarm), respectively. This allowed me to track obtained sensitivities against a set minimum performance level.

Statistics

I conducted a univariate Analysis of Variance with one between-subject factor and three repeated measures factors using SPSS (PASW Statistics 18, 2009). A factorial model was chosen to determine the main and interaction effects of target reverberation level, vocalization type, and level of background noise on the subject's performance (represented by d'). Species served as the independent, i.e. between-subjects factor, which divided all subjects into groups. I tested homoscedasticity by using Levene's Test of Equality of Error Variances for the

between-subject factor and Mauchly's Test of Sphericity for within-subjects factors. I additionally inspected Spread-versus-Level Plots that graph standard deviations against factor level means. The data fulfilled the assumptions of being normally distributed and having equal variances across factor levels. In cases where sphericity was violated I used Greenhouse-Geisser adjustments. Post-hoc Bonferroni-adjusted multiple comparisons were performed to compare the birds' performances across all factor levels (including between-subjects factor) and identify significant differences. For this purpose, level means within each factor were compared using 95% confidence intervals (CIs) with Bonferroni-adjustment.

3.3.3 RESULTS

Performance for target stimuli without reverberation, i.e. 0 ms reverberation time, served as control and was consistently at or above criterion level ($d' \geq 3.0$), which corresponds to a hit and false alarm rate of ≥ 0.95 and ≤ 0.1, respectively (see 3.3.2 "Methods"). Of the three main within-subject factors noise and target reverberation times (NL and RL) had the most significant effect on the birds' ability to discriminate between vocalization sets from different individuals (Table 2). Species as the between-subjects factor (SP) also was a significant contributor and in fact caused more of the overall data variation than vocalization type (partial eta-squared $\eta^2 = 0.697$ (SP) compared to $\eta^2 = 0.462$ (VT)), even though the latter was more significant. Most of the observed data variation, however, was primarily attributed to reverberation as a factor, followed by noise levels ($\eta^2 = 0.995$ (RL);

η^2 = 0.957 (NL)). Post-hoc multiple comparisons using Bonferroni-adjusted 95% CIs revealed that budgerigars showed a higher perceptual sensitivity (as indicated by the larger mean value for d') compared to either of the other two species, whereas canaries appeared to perform worst and on average just below d' = 2.0 (Figure 3), which is equal to hit and false alarm percentages of e.g. (HIT/FA) = (50/2) (see 2.2.5 "Measuring Auditory Sensitivities in the Lab"). This difference, however, was only significant between budgerigars and canaries.

Table 2. Repeated Measures ANOVA showing univariate results for between- and within-subjects effects and their interactions (α = 0.05). The model uses Type III Sums of Squares. *Greenhouse-Geisser adjustment of values where sphericity could not be assumed. Discrimination between stimuli depended mostly on (in descending order) reverberation, noise, species, the interactions between vocalization and reverberation, and between species and reverberation.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Between-Subjects*					
Species	2	74.774	37.387	6.905	0.028
(2) *Within-Subjects*					
Vocalization	*2.571	94.640	*36.812	5.153	*0.014
Noise	2	241.543	120.771	134.103	<0.001
Reverberation	7	979.547	139.935	1314.956	<0.001
(2) *Interactions*					
Vocalization x Noise	16	13.440	0.840	1.156	0.318
Vocalization x Reverberation	*4.886	19.250	*3.939	3.821	*0.009
Noise x Reverberation	*3.029	2.503	*0.826	2.472	*0.094
Species x Noise	4	5.363	1.341	1.489	0.266
Species x Vocalization	*5.142	95.708	*18.614	2.605	*0.066
Species x Reverberation	14	3.408	0.243	2.287	0.020
Vocalization x Noise x Reverb.	*5.034	11.692	*2.323	1.882	*0.127
Species x Vocalization x Noise	32	32.200	1.006	1.385	0.115
Species x Reverberation x Noise	*6.057	3.702	*0.611	1.829	*0.149
Species x Reverb. x Vocalization	*9.773	15.776	*1.614	1.566	*0.168

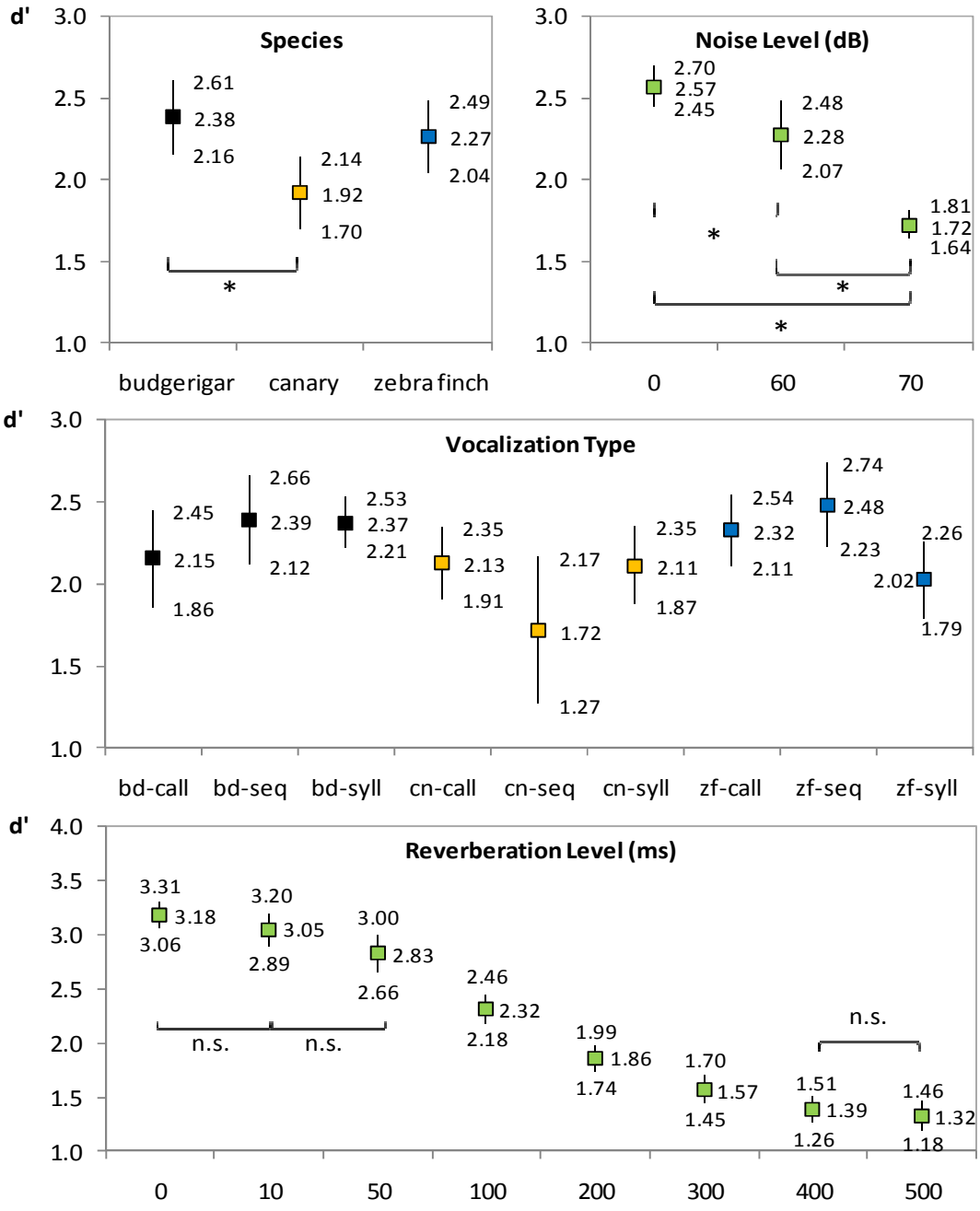


Figure 3. Significant main effects showing 95% Bonferroni-adjusted confidence intervals around estimated marginal means. Discrimination was easiest for budgerigars and zebra finches and without noise. The latter decreased average performance almost linearly by a d' of 0.85. Among budgerigar and zebra finch vocalizations short song excerpts (seq) were easiest. Discrimination became increasingly harder for more highly reverberated targets, decreasing performance by a maximum d' of about 2.0 but remaining above d' = 1.0. For "Species" and "Noise Level (dB)" significant differences between factor levels are marked with *. For "Reverberation Level (ms)" only non-significant differences are indicated (n.s.). (Vocalization abbreviations: bd = budgerigar, cn = canary, zf = zebra finch; call = call, seq = song sequence, syll = syllable.)

Although not significant, there was a general tendency for birds to be less sensitive to differences between canary vocalizations, with the exception of the budgerigar call and the zebra finch syllable that yielded similar means for d' (barely above 2.0) like the canary call and syllable. Perceptual sensitivity toward sound differences declined with increasing reverberation level of the target, but only at overall moderate levels an increase in reverberation actually caused a significant decline in sensitivity as indicated by the sigmoid shape of the curve in Figure 3. Compared to the quiet condition, adding white noise at a level of 60 dB SPL (21.3 dB spectrum level) did not decrease the birds' average sensitivity to or below 2.0 (Figure 3), while noise at a level of 70 dB SPL (31.3 dB spectrum level) did. Figure 4 (b), however, illustrates that d' levels of less than 2.0 are reached even for the no noise condition when reverberation times are 300 ms or above. In contrast, a reverberation time of only 100 ms is sufficient to reach similarly low performance levels under conditions with 70 dB noise. Note, however, that most performances are still above d' = 1.0, which is a more liberal sensitivity yardstick against which to track performances that are still considered to be above chance (see 2.2.5 "Measuring Auditory Sensitivities in the Lab").

The interaction effect between type of vocalization and reverberation level is significant, but Figure 4(a) indicates that the apparent statistical significance could be attributed to rather random variation, brought about by the large number of combined factor levels (9 x 8 = 72 level combinations). Therefore, this result should be treated with caution in subsequent interpretations. Noise and

reverberation time do not show any significant interaction, but Figure 4(b) illustrates that sensitivity toward stimulus differences at high levels of noise is significantly different from the birds' sensitivity toward these differences at lower levels or no noise. Figure 6 exemplifies the relation between d' and correct responses by showing results for the percentage of correct discrimination of stimuli for the interaction effect noise x reverberation and should be compared with Figure 4(b). Since differences in the percentage of Hits between noise levels are rather small, changes in % FA (false alarms) must be correspondingly larger and account for most of the resulting difference among d' for different noise

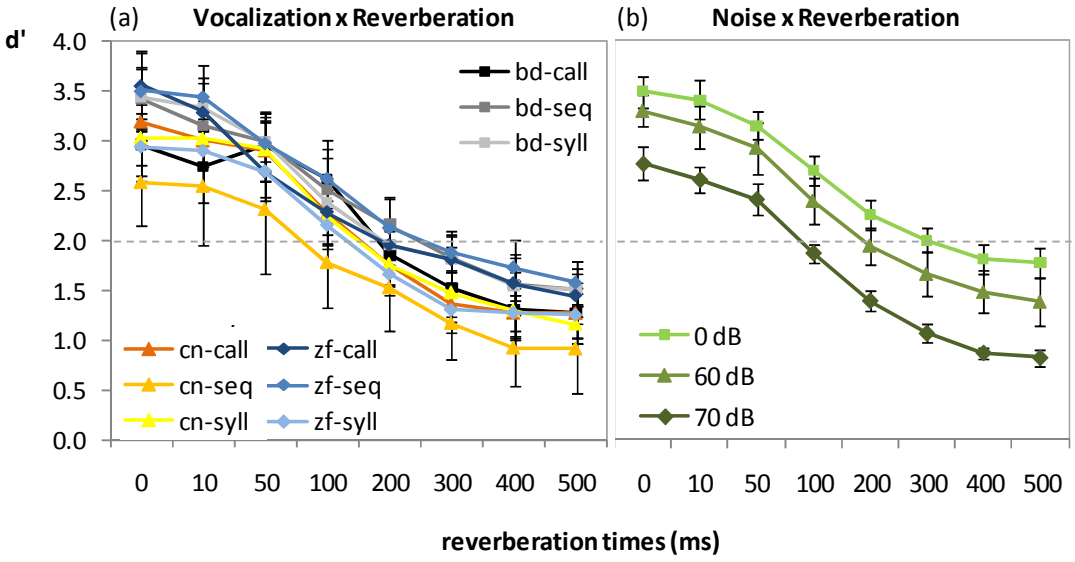


Figure 4. Interaction effect between (a) type of vocalization and reverberation time (significant), and (b) noise and reverberation time (non-significant). Differences in canary sequences (short song excerpts) were consistently hardest to distinguish. Differences in performance between noise levels are similar across and thus independent of reverberation time. High noise and reverberation times decrease performance from between 2.8 and 3.5 to d' ≤ 2.0 (stippled line) or even ≤ 1.0. Bars represent Bonferroni-adjusted 95% CIs around estimated marginal means.

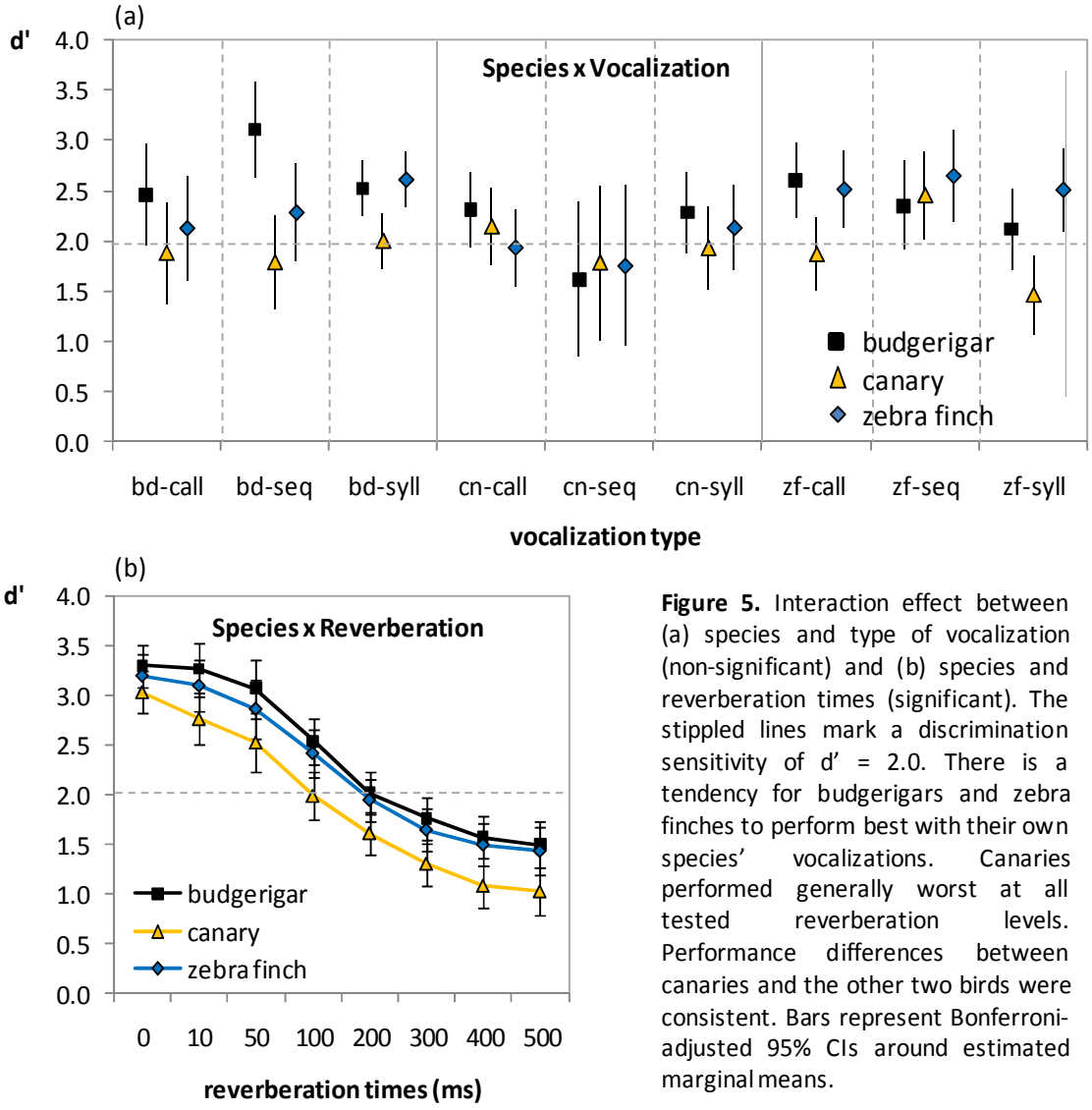


Figure 5. Interaction effect between (a) species and type of vocalization (non-significant) and (b) species and reverberation times (significant). The stippled lines mark a discrimination sensitivity of d' = 2.0. There is a tendency for budgerigars and zebra finches to perform best with their own species' vocalizations. Canaries performed generally worst at all tested reverberation levels. Performance differences between canaries and the other two birds were consistent. Bars represent Bonferroni-adjusted 95% CIs around estimated marginal means.

levels. Generally, an increased number of responses to the wrong stimuli while maintaining hit rate at a rather constant level indicates higher perceived similarity between the tested vocalizations. The interaction effect between species and vocalization is non-significant, but results show a slight tendency toward species

performing best with their own vocalization when that vocalization is a longer sequence of song syllables (Figure 5(a)). However, Figure 5 (b) shows that canaries generally exhibit a consistently lowest sensitivity for discrimination across all reverberation times without any species-specific advantage.

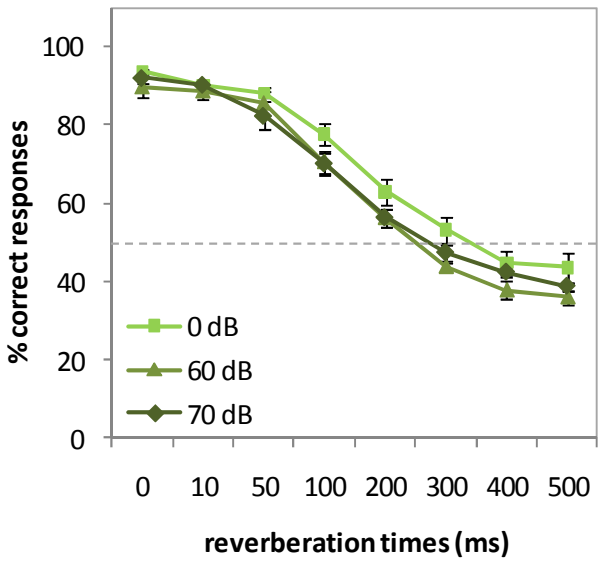


Figure 6. Interaction effect between noise and reverberation time showing the percentage of correct responses (HITS) as dependent variable instead of d'. It illustrates what changes in d' in Figure 4 (b) mean in terms of % correct responses to targets. Response percentage clearly drops below 50% (stippled line) already at 300 ms reverberation time when noise is present. Hits below 50% are also obtained under conditions without noise but at slightly higher reverberation time. Bars represent Bonferroni-adjusted 95% CIs around estimated marginal means.

Taken together, the results indicate that under any condition, the birds could not correctly discriminate between similar stimuli at a higher d' than 2.0 when stimuli were reverberated at times around and above 200 ms. The addition of noise had a further deteriorating effect on the birds' sensitivity toward audible individual differences within the vocalizations. Budgerigars generally performed best, but there was no clear species-specific advantage in the discrimination of conspecific vocalizations for either of the three tested species.

3.3.4 DISCUSSION

The aim of this experiment was to investigate reverberation and noise effects on the discrimination of similar, but individually distinct, vocalizations in the budgerigar, canary, and zebra finch. Distinctions had to be made between the repeating background of one individual's vocalization (B) and a randomly inserted similar target vocalization from a different individual (A). Given the design of this study, in which background and target stimuli each consisted of sets of one individual's vocalization at several reverberation times, it was important to ascertain that birds indeed had learned to generalize across reverberation times and that a shift in feature weighting toward structural details common to all variations in a set had occurred. To that end, I hypothesized that if birds were merely habituating to or memorizing the sounds of each set with their respective reverberation times, they should not exhibit any difficulty in discriminating individual A's and B's vocalization, no matter at what reverberation level individual A's vocalization (target) was presented. On the other hand, if the birds' performance did vary with the degree to which the target was reverberated, one could assume that the aforementioned feature weighting has actually taken place and the birds recognize the overall similarity of individual B's reverberated vocalization. The reported results clearly support the latter hypothesis and can thus safely be interpreted based on the assumption that birds discriminated individually distinct features common to all vocalizations in the repeating background from features of the target sounds.

In line with the arguments stated above, results show a strong dependence of discrimination abilities on the combined levels of reverberation and simultaneous background noise, implying communication challenges on the part of both signalers and receivers. This corresponds well with numerous human studies that have demonstrated increased detrimental effects of reverberation on speech recognition when noise was added (e.g. Harris and Reitz 1985; Harris and Swenson 1990; Helfer and Wilber 1990; Gordon-Salant and Fitzgibbons 1995a). Generally speaking, reverberation can obliterate or completely remove information encoded in a signal, while noise simply masks it. In reverberant noisy environments a signaler therefore may encounter difficulty in getting its identity across, while the receiver may have trouble with both detecting and discriminating signalers as well as decoding the information contained in the signal. Based on the experimental design of this study, however, the results allow conclusions only on relatively short vocalizations and should not be generalized across longer sequences of vocalizations, such as the songs of songbirds and the often several minutes long songs or warbles of budgerigars. Songs, in particular, serve long-range communication in the wild to advertise information regarding species, sex, identity, intentions, and status (Catchpole and Slater 1995). A characteristic feature of such vocalizations therefore is the loudness and the so-called serial redundancy or repetitiveness with which they are produced (Brumm and Slabbekoorn 2005). In fact, under noisy conditions many animal species are known to increase the loudness of their signals (the Lombard Effect) and adjust their

serial redundancy (Potash 1972; Lengagne et al. 1999; Brumm 2004). This signaler behavior is thought to have evolved to resist the deterioration or loss of the intended message, which is costly for both signalers and receivers (Catchpole and Slater 1995), although it has been suggested that not all information transfer benefits from increased redundancy (Brumm and Slabbekoorn 2005). On the signaler's part, the production of loud, repetitive signals is energetically costly, while on the receiver's part, making behavioral decision based on 'wrong' information can result in for example decreased female reproductive success, which greatly depends on choosing a high quality male of the correct species or telling own offspring apart from those of others. It is therefore possible that the birds' discrimination improves, once reverberated signals are long and repetitive, a condition I have not tested in this study. In the case of calls, however, receivers have to make quick behavioral decisions in response to signals of rather short duration, and a co-evolutionary adaptation of both call features and perceptual abilities to resist sound-degrading conditions could have been expected. However, I did not find performance to be particularly good or any better than in response to the other tested signals. In fact, the results indicated a slight (but non-significant) tendency toward budgerigars and canaries performing best with their own vocalization when that vocalization is a longer sequence of song syllables (Figure 5(a)). It is unlikely though that increased temporal integration was the cause of the slightly better discrimination, because temporal summation and integration functions do not change much beyond durations of about 200 ms in

small birds (Dooling 1979; Dooling and Searcy 1985). More probable, it could indeed be due to an increase in overall redundancy of information in the presence of several syllables, which may have aided discrimination. The reason for why this added information did not produce significant differences in performance may be attributed to the still quite short duration of the tested song excerpts (500-600 ms). The observed differences could have proven significant had the tested song sequences been of longer duration. It is further interesting that calls were relatively hard to discriminate compared to song sequences and single syllables with the exception of the canary call. It seems plausible that a high sensitivity toward calls even under deteriorated acoustic conditions should be highly adaptive, especially if contexts in which calls are used are greatly dependent on individual discrimination and recognition. One possible explanation for the present, somewhat counterintuitive findings is that although the chosen calls were all contact calls and should be highly distinguishable, these vocalizations are frequently produced at close range when visual cues ought to be available. The information contained in both the vocal and visual stimulus could then be combined to serve as a much enhanced cue to the identity of the signaler. In many social interactions, multimodal signals are common and greatly increase efficacy and improve accuracy of the exchanged messages. In humans, for instance, such cross-modal use of signals to improve speech perception occurs during combined listening and lip reading (MacDonald and McGurk 1978; Grant and Seitz 2000; Besle et al. 2004). Many animal calls also often serve more general functions in

contexts where effective warnings about ensuing aggressive behavior or nearby threats are not dependent on conveying individual identity.

Overall, budgerigars seemed to have the competitive edge in the discrimination of similar stimuli under noisy, reverberant conditions, but there was no evidence of a clear species-specific advantage in the ability to discriminate conspecific stimuli across all three vocalizations types. Again, this could be due to the limited number of vocalizations that were tested and the relative short duration of each of the vocalizations. However, of the tested species the auditory system of budgerigars is known to have the greatest spectral resolution (Dooling and Saunders 1975; Okanoya and Dooling 1987), which may be linked to this species' increased sensitivity toward distinctive sound features despite reverberation and noise. If individually distinct sound features are contained in both the temporal and frequency domain, and if reverberation obliterates much of the information encoded in the temporal fine structure, then relying on spectral content instead may be the best alternative, giving budgerigars an advantage over other species.

Compared to the nearly perfect performance under conditions without reverberation or noise, perceptual sensitivity toward individually distinct characteristics of the sounds decreased to or below d' = 2.0 even at moderate reverberation times of about 200-300 ms but stayed mostly above d' = 1.0. Both d' values are equal to hit rates of e.g. 0.5 and rather low false alarm rates (0.02 and 0.16, respectively) (see 2.2.5 "Measuring Auditory Sensitivities in the Lab"),

indicating that the tested perceptual task was still feasible but required more effort. In other words, it seems obvious that fine structural details within the vocalizations are important in individual discrimination but were somewhat obliterated by reverberation and masked by noise, making this task considerably harder but not entirely impossible. Potential duration cues, too, were likely rendered less reliable, as echoes elongated both the entire signal and single song syllables, and thus potentially reduced duration differences between the sounds and the silent gaps within song excerpts. This bears important implications for species that exhibit song sharing or other forms of vocal imitation and engage in social behaviors that are mediated by individual recognition (Catchpole and Slater 1995). As discussed earlier, the proposed fitness consequences arising from a decreased ability to reliably discriminate individually distinct sounds in reverberant and noisy environments may in fact be alleviated by utilizing other modalities in combination with vocal signals in the wild. In addition, vocal redundancy which is frequently observed in highly sound-degrading and -masking environments but is not reproduced in this experiment may help vocally mediated recognition.

Future Directions

First, to evaluate the role of serial redundancy on overall signal resistance to combined reverberation and noise effects, birds should be tested with signals with varying duration and repetitiveness, since repetitiveness of long-range vocal signals is widespread among vertebrates and invertebrates alike (e.g. crickets,

frogs, and mammals). Signal redundancy is not necessarily a way of adapting to dynamic, sound-modifying environments in humans, who instead may increase the loudness or decrease the speed with which they speak.

Second, recognition errors in mating contexts usually result in higher fitness costs for females than for males (Searcy and Brenowitz 1988; Catchpole and Slater 1995; Ratcliffe and Otter 1996), especially in songbirds. It can therefore be assumed that sex differences may exist, with females being more discriminating than males. This study used both males and females as test subjects and was designed in such a way as to eliminate gender differences as a confounding factor (see "Methods"). Future studies could be designed to address the specific goal of investigating gender differences in discriminating similar vocalizations under conditions with varying noise and reverberation times.

Third, to be able to extrapolate results to conditions in the wild, noise maskers with spectra typical of environmental (biotic or abiotic) noise sources should be used (Lohr et al. 2003, Brumm and Slabbekoorn 2005) in combination with much higher reverberation times than the ones I tested in this study.

3.4 Study IV

Forming auditory objects in a cocktail party setting – The impact of acoustic reverberation

3.4.1 INTRODUCTION

In acoustic environments with multiple signalers, it is pivotal that listeners can selectively attend to and follow sound sequences of one sender while disregarding those of others. One critical aspect of auditory scene analysis thus involves the perceptual parsing of acoustic sequences into separate "streams" or "objects" (Bregman and Campbell 1971; Hartmann 1988; Bregman 1990; Yost 1991; Carlyon 2004). In other words, the auditory system has to be able to attend to and organize specific unitary sound components from one source into single streams or objects based on their common physical characteristics (stream *integration*) while separating them from components arising from other sound sources with different unifying features (stream *segregation*) (Sussman 2005).

Ever since 1950, human psychophysical studies have been pivotal in understanding auditory scene analysis as a solution to the so-called "cocktail party effect" (e.g. Miller and Heise 1950; Bronkhorst 2000; Carlyon 2004), and studies of sound perception in songbirds strongly suggest that auditory scene analysis plays a significant role in vocal communication also among vertebrate animals, including birds (Hulse et al. 1997; Wisniewski and Hulse 1997; Fay 1998; MacDougall-Shackleton et al. 1998; Benney and Braaten 2000; Moss and Surlykke 2001; Hulse 2002; Izumi 2002; Barber et al. 2003; Bee and Klump 2004; Fishman et al. 2004;

Bee and Klump 2005; Micheyl et al. 2005; Bee and Micheyl 2008). It is thought to be an important function of the auditory system that helps listeners, human and non-human, to function and, in the case of animals, survive in social contexts with multiple sound sources. The ability to analyze an acoustic scene is a shared capacity of all vocally communicating species and ultimately contributes to fitness. Indeed, it appears to have initially evolved in long extinct species based on the fundamental need to localize and distinguish relevant from irrelevant sound sources for decisions on context-appropriate behaviors (Fay and Popper 2000; Fay 2007).

The segregation and integration of auditory objects is achieved by complex sound processing and cognitive integration. In essence, the physical features of the acoustic environment are represented by a neural code that conveys information about the sound signal and is integrated with prior sensory experience and other simultaneous sensory input. This then leads to the listener's perception of its acoustic surroundings and, potentially, appropriate behavioral responses. The auditory system uses a variety of cues to integrate different components of a temporally varying frequency spectrum into a coherent auditory stream. Some of the cues are acoustic components that have common onset and offset times, common amplitude modulations, as well as similar frequency ranges and spatial location (Bregman and Campbell 1971; Bregman 1990; Vliegen and Oxenham 1999). In complex acoustic scenes with multiple sound sources, spatial cues may be a less useful cue (Cusack and Carlyon 2004), especially if the direction

of incoming sound waves is changed when signals are reverberated. Moreover, although the integration and segregation of auditory objects is aided by a variety of acoustic cues, the ability of the auditory system to identify and segregate objects successively may be compromised when signal degradation caused by reverberation is high. An acoustic scene of reverberated stimuli is less likely to provide distinctive and reliable grouping cues in that tails of echoes and the interaction between direct and reflected sound waves can 'smear' sharp onset and offset times and obliterate or change the fine temporal structure of sounds. Depending on the severity of these reverberations, this could negatively affect the reliability of cues such as common amplitude modulations across the frequency spectrum and onset and offset times. In addition, frequency-dependent effects of reverberation change the signal's spectral patterns and may deteriorate strong frequency characteristics, while masking from noise will simply remove some grouping cues (Klump 1996; Cusack and Carlyon 2004). It is therefore important to ask if two or more auditory streams are more likely to be fused as a consequence of signal reverberation under conditions with increasing numbers of simultaneous signalers. Seen from a listeners perspective whose aim it is to attend to and differentiate the vocal messages of one or more individuals from a background of competing signals, individual discrimination is hindered not only by the increased vocal similarity that reverberation can cause (see Study III). Discrimination may also be affected by the auditory system's inability to separate vocalizations of one

individual or species from those of others in the form of a separate acoustic object, even if these are very different.

Previous studies on auditory scene analysis in birds *and* humans have used competing signals that were *not* reverberated but provided well-conserved grouping cues (e.g. Alain et al. 2001; Bee and Klump 2004; Cusack et al. 2004; Bee and Klump 2005). The objective in this study therefore is to test whether the auditory system's ability to segregate acoustic streams is compromised when a complex acoustic scene with multiple signalers contains reverberated signals. I tested the working hypothesis that a target auditory object or stream is less likely to be segregated from competing signals when sounds are reverberated and thus less likely to provide distinctive auditory grouping cues. I designed a psychophysical experiment with budgerigars, canaries, and zebra finches, in which subjects were tested with biologically relevant vocalizations of either their own or the two other species' typical repertoire. In order to force birds to attend to an entire sequence of song rather than just to its onset, birds were initially trained to respond to a longer song sequence from one particular individual, while withholding a response to the same song with a slight spectral, temporal or compositional change toward the end. Subsequent testing involved a GO/NOGO procedure, in which the birds had to continue responding to one but not the other sequence (GO or NOGO song) either in the absence (control) or presence of other superimposed songs from one, two or four different individuals. Tests were repeated with five reverberation times (including no reverberation), and after

completion new training was required to allow for tests with a new set of stimuli from a different species. If reverberation complicates stream segregation, the birds ought to perform worse with increasing reverberation times, i.e. either respond less often to the GO song or make more mistakes in discriminating between GO and NOGO song. Of course, the degree to which auditory stream segregation is compromised likely depends on the degree to which sounds are reverberated as well as the spectral distribution and bandwidths of both the irrelevant background songs and the actual target song.

3.4.2 METHODS

Subjects

Four budgerigars (2 males, 2 females), four canaries (all males), and four zebra finches (2 males, 2 females) were used as test subjects. Zebra finches were offspring from birds obtained from commercial dealers, while budgies and canaries were first generation birds from dealers. All birds had normal, species-specific auditory tuning curves and had obtained extensive experience with reverberated sounds by partaking in all or some of the previous studies. Birds were housed in individual cages in a vivarium at the University of Maryland and kept at a constant light-dark cycle to avoid potential season-induced changes in hearing abilities. They were fed daily with standard parakeet, canary, and finch seed mixes and reinforced with yellow millet during experimental sessions. The

weight of the birds was monitored and kept between 85 and 90% of their free-feeding weight.

Apparatus and Psychophysical Task

Subjects were tested in a psychophysical set-up consisting of a customized operant-conditioning chamber in a sound-attenuated booth (Industrial Acoustics Company, Inc., Bronx, New York, USA). The chamber consisted of a wire cage (approx. 25 cm^3) with a food hopper for access to food and a response panel made up of two horizontally aligned LED keys attached to micro-switches (for details see Park et al. 1985; Dooling and Okanoya 1995a). Experimental events and sound playback were controlled by a computer and Tucker-Davis Technologies (TDT, Gainsville, FL) System III modules the same way as described in Study I.

As in Study II, the bird were tested in a GO/NOGO Classification Task, in which either a GO or a NOGO stimulus is presented upon initiation of a trial and the bird is required to give (GO) or withhold (NOGO) a response. The GO and NOGO stimuli are comparable to respectively the target and background stimuli in an Alternating Sound Task, except that in the classification task, the GO stimulus is not compared to a continuously repeated background of the NOGO stimulus. Instead, GO and NOGO stimuli are presented separately and at random once the bird initiates a trial. Thus, in contrast to the Alternating Sound Task, a bird is required to hold the GO and NOGO stimuli in long-term memory and give or withhold a response depending on the presented stimulus.

Stimuli & Reverberation Model

Test stimuli consisted of 4-s sequences of natural vocalizations (songs) recorded from unfamiliar individuals of each of the three tested species. Recording were made with a directional microphone (Audio-Technica Pro 35ax) and a Marantz PMD670 digital recorder at a sampling frequency of 48,000 Hz (16 bit). The vocalization sequences comprised budgerigar warbles, zebra finch song, and canary songs with typical spectro-temporal pattern. All sequences were band-pass filtered at 0.5-8 kHz, which eliminated any ambient background noise present at very low or high frequencies and only covered the birds' average hearing range. The frequency ranges of each species' sequence were 0.5-8 kHz, 1-3.5 kHz, and 0.5-8 kHz for budgerigar, canary, and zebra finch vocalizations, respectively. The budgerigar sequence was a 4-s warble sequence with a variety of different syllables, while the canary song consisted of a 4-s trill with frequency modulation. The zebra finch song was a 4-s sequence of repeated motifs with natural inter-motif intervals of no more than 200 ms.

The GO stimulus consisted of the complete, natural sequence, whereas the NOGO stimulus was made up of the same GO-stimulus sequence with a slight spectral, temporal or compositional change lasting ca. 1.5 s towards the end of the sequence, i.e. starting at about 2.5 s (Figure 1). I chose this design to force the test subjects to perceptually follow or attend to the sequence to its very end before making a response decision (i.e. withholding or giving a response). In the budgerigar song, the last few song syllables were replaced by a different type of

syllable of the same duration. This way I was able to mostly maintain the frequency and temporal pattern typical of natural budgerigar songs while changing the song's syllable composition (Figure 1a). The last 1.5 s of the canary trill sequence was interspersed with two gaps of silence of 400 ms that were separated by 350 ms while preserving the frequency and composition of the remaining trill chunks (Figure 1b). In the case of the zebra finch NOGO stimulus, the change comprised a gradual, 1 kHz spectral bend (or dip) of the last motif sequence while preserving the song's syllable composition and most of its temporal structure (Figure 1(c)). Note that changes in composition also had slight spectral effects, and the described frequency bend resulted in a 20 ms longer motif because of its decreased frequency, which was less than a 2% change in duration.

The continuous background consisted of a 2-min loop of coherent, natural songs from one, two, or four other unfamiliar birds of the same species or no song (control). In background loops with more than one vocalizing bird, the song sequences randomly overlapped each other in time and frequency with intermittent silences of no longer than 50 ms (Figure). In background loops with only one song sequence, silences between song syllables never exceeded 500 ms. Transient fluctuations in maximum amplitude for more than 0.5 s were digitally normalized and adjusted to equal peak RMS values to avoid fluctuating Signal-to-Noise-Ratios of the GO or NOGO stimuli during experiments. Additionally, all stimuli (background loops and GO/NOGO stimuli) were calibrated using a Larson-

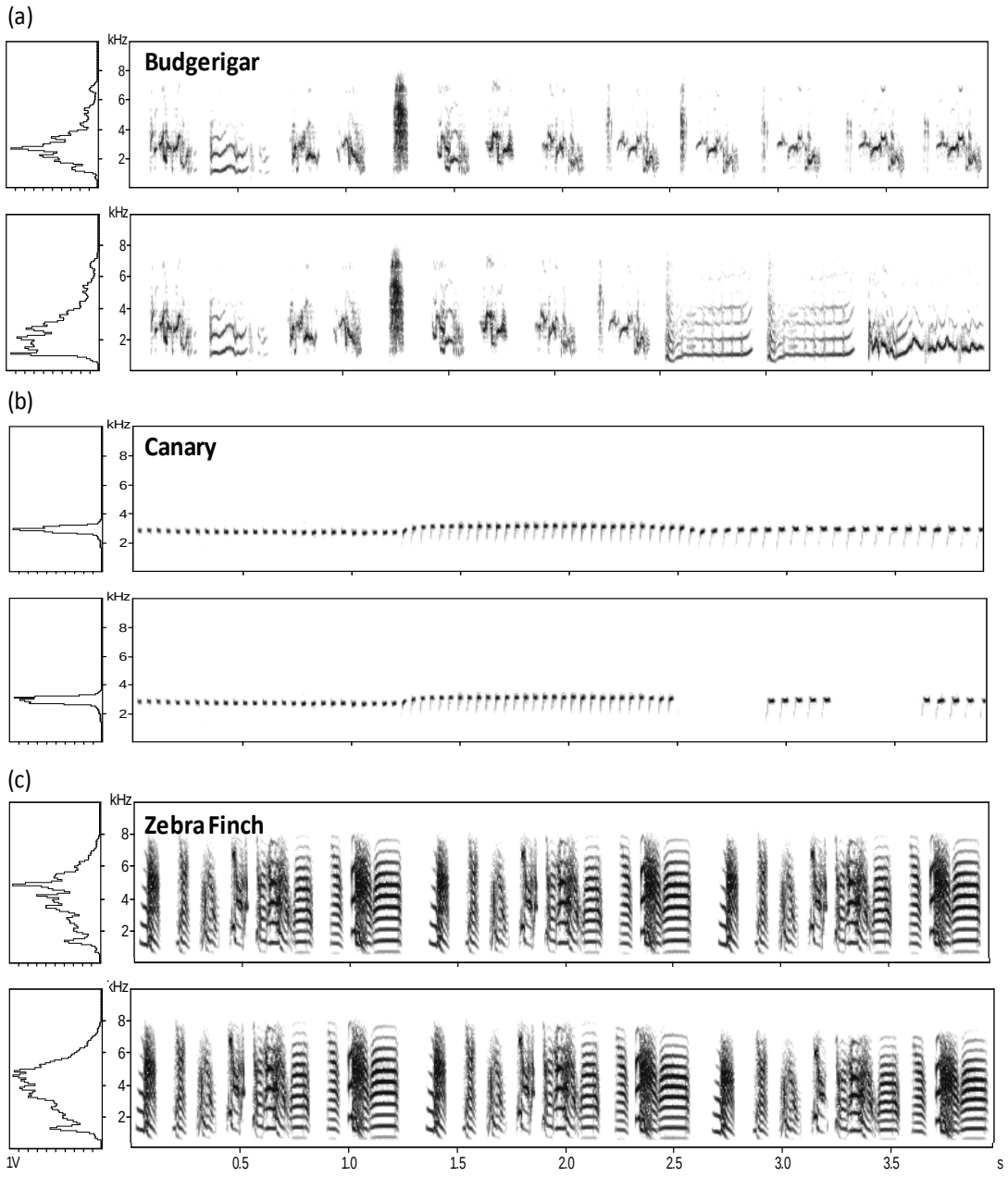


Figure 1. Spectrograms of GO and NOGO sequences of budgerigar (a), canary (b), and zebra finch (c) song, with frequency (in kHz) on the y- and time (in s) on the x-axis. The first sequence of each pair is the unaltered GO version, the second sequence the NOGO version of the song that contains compositional (a), temporal (b), or spectral (c) changes within the last 1.5 s of the song. The duration of each sequence is 4 s. The frequency boundaries of each spectrogram are at about 0 and 8.5 kHz. To the left of the spectrogram is the frequency or power spectrum (in V) that shows the distribution of acoustic energy across frequencies.

Davis System 824 sound level meter (A-filter weighting, fast response) with a 1/2" microphone mounted inside the cage in the same position and direction as thebird's head. I took the largest measure of the maximum A-weighted root-mean-square (RMS) level and subsequently normalized all sound sequence levels to a standard amplitude of 70 dB (A, supra-threshold level). This is a comfortable listening level for birds and equivalent to a bird singing at a distance of about 10 m (source level: 90 dB). Continuous background and GO/NOGO sequences were played back at the same level and at a sampling frequency of 24,414 Hz.

All stimuli (including background sequences) were artificially reverberated at 0, 100, 200, 400, and 800 ms using the same Matlab 7.5.0 (R2007b, The Mathworks Inc. 2007) algorithm described in Study I (exponentially decaying impulse response using Gaussian noise). Here, the tails of echoes were preserved to account for within-stimulus changes as well as signal elongations and their potential forward-masking effects. As in my previous studies (Study I-III), a reverberation time of 0 ms was used to create the non-reverberated sound, thereby avoiding detectable differences due to differences in the type and amount of signal processing alone. In test sessions the background sequence and the GO and NOGO stimuli were always presented at the same reverberation times.

Psychophysical Task – Training & Testing

Training phase 1: The birds I chose for this experiment had all previously been tested for hearing deficiencies and subsequently trained in an Alternating Sound Task (see Study I and III), in which they had to detect a change in a continuously

repeated 'background' sound. For this experiment and the one described in Study II, a GO/NOGO psychophysical procedure with selective playback options for GO, NOGO and PROBE stimuli was implemented in Matlab 7.5.0 to control the experimental events via Tucker-Davis System III's software interface. The birds were trained to initiate the onset of one of two possible sound stimuli by pecking the green observation LED and subsequently give or withhold a response depending on the stimulus type. The onset was delayed by 50 ms to avoid pecking noises from overlapping with stimulus playback. For initial training purposes the durations of the response interval was set to 4 s and then gradually decreased to 1.5 s (post-playback). Birds were required to respond to the GO stimulus by pecking the red report LED, while withholding a response upon hearing the NOGO stimulus. The GO and NOGO stimuli consisted of a conspecific, 200-300 ms long syllable and a syllable of similar duration from a different species (heterospecific syllable), respectively. Only correct responses to the GO stimulus (hits) were rewarded with 2 s access to food. If the birds hit the report key when the NOGO stimulus was played back, all lights in the chamber were turned off for 15 s (blackout). If no response followed the presentation of either stimulus (i.e. correct rejections of the NOGO stimulus or missed responses to the GO stimulus), the session proceeded to the next trial. A complete training session consisted of 100 trials with 50 GO and 50 NOGO trials presented in random order with a maximum of 4 consecutive GO or NOGO trials. Birds ran up to 3 sessions a day with a single session lasting about 20-60 min. Once the birds reached my criterion of at least

95% hits and correct rejections in two consecutive sessions (corresponding to d' ≥ 3.3), they proceeded to training phase 2.

Training phase 2: This training phase was the longest and most challenging phase. It involved three sets of shorter versions of the final stimuli that were used in the experiments (see "Stimuli and Reverberation Model" above for details on the sound sequences). GO and NOGO stimuli were shortened to a duration 1 s, 2 s, and 3.5 s, while 500 ms of the aforementioned change was preserved towards the end of the NOGO stimulus. The birds were trained with progressively longer stimulus pairs to overcome the challenge of not immediately and exclusively giving a response right at the onset of a stimulus but waiting until the end of playback. This was additionally achieved by having the response parameters in the program set to ignore all key pecks during stimulus playback and record and respond to only those given during the post-playback response interval (now set to 1.5 s). In other words, if a GO stimulus was presented and a bird pecked the report key only at the beginning of playback or repeatedly until the end of the sequence but then stopped responding post-playback, no food reward was given. The long 'waiting behavior' that I was trying to achieve by this training paradigm is a rather unnatural behavior especially when birds are highly motivated to obtain food, so the time it took to reach criterion (as defined in "Training phase 1") varied greatly among birds and seemed to depend on their overall day-to-day motivation. However, once they were trained successfully at each stimulus duration level, the overall performance was stable. As in "Training phase 1", a

complete session consisted of altogether 100 trials with 50 GO and 50 NOGO trials presented in random order with a maximum of 4 consecutive GO or NOGO trials. Because of the more challenging nature of this training phase and the frequent occurrence of frustration-induced displacement behaviors, birds ran only a maximum 2 sessions a day with a single session lasting about 20-60 min. Once birds achieved criterion performance of at least 95% hits and correct rejections in three consecutive sessions (corresponding to d' ≥ 3.3), they proceeded to the experimental phase.

Experimental phase: The birds were first given a few initial training sessions with the final 4-s long, non-reverberated GO/NOGO stimulus pairs to reach stable performance above criterion for 300 trials in a row. No continuous background was played. All three species started with their own species' song sequences at all possible treatment combinations, starting with the "no background – no reverberation" condition (control), and then continuing in random order with the other conditions. Once all combinations were tested, the birds were moved to "Training phase 2" for a different species' vocalization and then, once completed, tested in the experimental phase (same procedure as above). This procedure was repeated one last time for the final pair of stimuli consisting of the remaining species' song.

Birds were tested for at least two sessions, across which birds had to show consistently stable performance. Only data from the last of these two sessions (i.e. a total of 100 trials) were used to obtain percentages for hits (correct positive

response to GO stimuli), misses (withheld response to GO-stimuli), correct rejections (correctly withheld response to NOGO stimuli), and false alarms (false positive response to NOGO stimuli). To allow for valid performance comparisons across species and conditions, I converted all hit and false alarm rates to the sensitivity index d' (for a "yes/no" task), which is based on relative z-scores for both hit and false alarm rates, i.e. standard deviation units of the normal distribution (see 2.2.5 "Measuring Auditory Sensitivities in the Lab", Appendix I, or Macmillan and Creelman 1991, 2005 for a stepwise guide for conversions to d').

Statistics

Statistical analyses were performed in SPSS (PASW Statistics 18, 2009). I conducted a univariate Analysis of Variance with one between-subject factor and three repeated measures factors. A full factorial model was chosen to determine the main and interaction effects of reverberation level, stimulus type, and number of background songs on the subject's performance (represented by d'). Species served as the independent, i.e. between-subjects factor, which divided all subjects into groups. The data fulfilled the assumptions of being normally distributed and having equal variances across factor levels. I tested homoscedasticity by using Levene's Test of Equality of Error Variances and Mauchly's Test of Sphericity for within-subjects factors. I additionally inspected Spread-versus-Level Plots that graph standard deviations against factor level means. Bonferroni-adjusted multiple comparisons were performed to reveal potentially significant differences between levels of all factors. Bonferroni adjustments reduce the probability of

committing Type I errors caused by multiple comparisons. This is a generally accepted procedure from a signal detection theory viewpoint (Macmillan and Creelman 2005) and corresponds well with recommended statistical analyses for repeated measures ANOVAs.

3.4.3 RESULTS

Performance for stimuli without reverberation, i.e. 0 ms reverberation time, and no simultaneous background songs served as control and was for all species consistently at or above criterion level ($d' \geq 3.3$), which corresponds to correct responses to GO and NOGO stimuli about 95% of the time (see 3.4.2 "Methods").

There was a significant effect of all main within-subject factors (vocalization type (VT), number of individuals singing in the background (BG), and reverberation time (RT)) as well the between-subjects factor species (SP) (Table 1). BG and RT, however, explained most of the variation in the dataset (partial eta-squared (η^2) values: 0.960 (BG) and 0.975 (RT) compared to 0.672 for VT and 0.837 for SP). Post hoc multiple comparisons using Bonferroni-adjusted 95% CIs revealed that performance was worst (i.e. d' lowest) for canary songs and decreased with increasing reverberation as well as progressively larger numbers of songs in the background (Figure 2). Compared to the quiet condition, adding only one simultaneous signaler in the background, however, did not have a significant negative effect on the birds' performance. Budgerigars showed a higher perceptual sensitivity as indicated by the significantly larger d' than either of the

other two species, whereas canaries appeared to perform worst. The ANOVA further revealed significant second-order interactions (Table 1), particularly between reverberation level and number of background songs (η^2=0.872). Interaction effects were also strong between species and vocalization type (SP x VT: η^2 = 0.630). Although interactions between species and reverberation level, and vocalization type and background were significant, these effects explained much less of the overall data variation (SP x RT: η^2 = 0.419; VT x BG: η^2 = 0.299). All remaining second-order interactions were not significant. Budgerigars achieved

Table 1. Repeated Measures ANOVA table showing univariate results for between- and within-subjects effects and their interactions (α = 0.05). The model uses Type III Sums of Squares. *Greenhouse-Geisser adjustment of values where sphericity could not be assumed. Some factors with greatest effects are (in descending order): reverberation time, background, interaction between reverberation time and background, species and vocalization.

Source	d.f.	SS	MS	*F*	Sig.
(1) *Between-Subjects*					
Species	2	10.663	5.331	23.083	<0.001
(2) *Within-Subjects*					
Vocalization	2	7.283	3.642	18.427	<0.001
Background	3	148.084	49.361	214.070	<0.001
Reverberation Time	4	153.231	38.308	344.490	<0.001
(2) *Interactions*					
Vocalization x Background	6	2.996	0.499	3.834	0.003
Vocalization x Reverberation Time	6	1.528	0.191	1.690	0.116
Reverberation x Background	*4.851	72.721	*14.991	61.165	*0.000
Species x Background	6	1.182	0.197	0.854	0.540
Species x Vocalization	4	6.055	1.514	7.659	0.001
Species x Reverberation	8	2.886	0.361	3.244	0.007
Vocaliz. x Backgr. x Reverb. Time	*7.235	7.628	*1.054	3.537	*0.003
Species x Vocalization x Backgr.	12	14.467	1.206	9.256	<0.001
Species x Reverb. Time x Backgr.	*9.702	6.081	*0.627	2.557	*0.017
Species x Reverb. Time x Vocaliz.	16	3.283	0.205	1.816	0.045

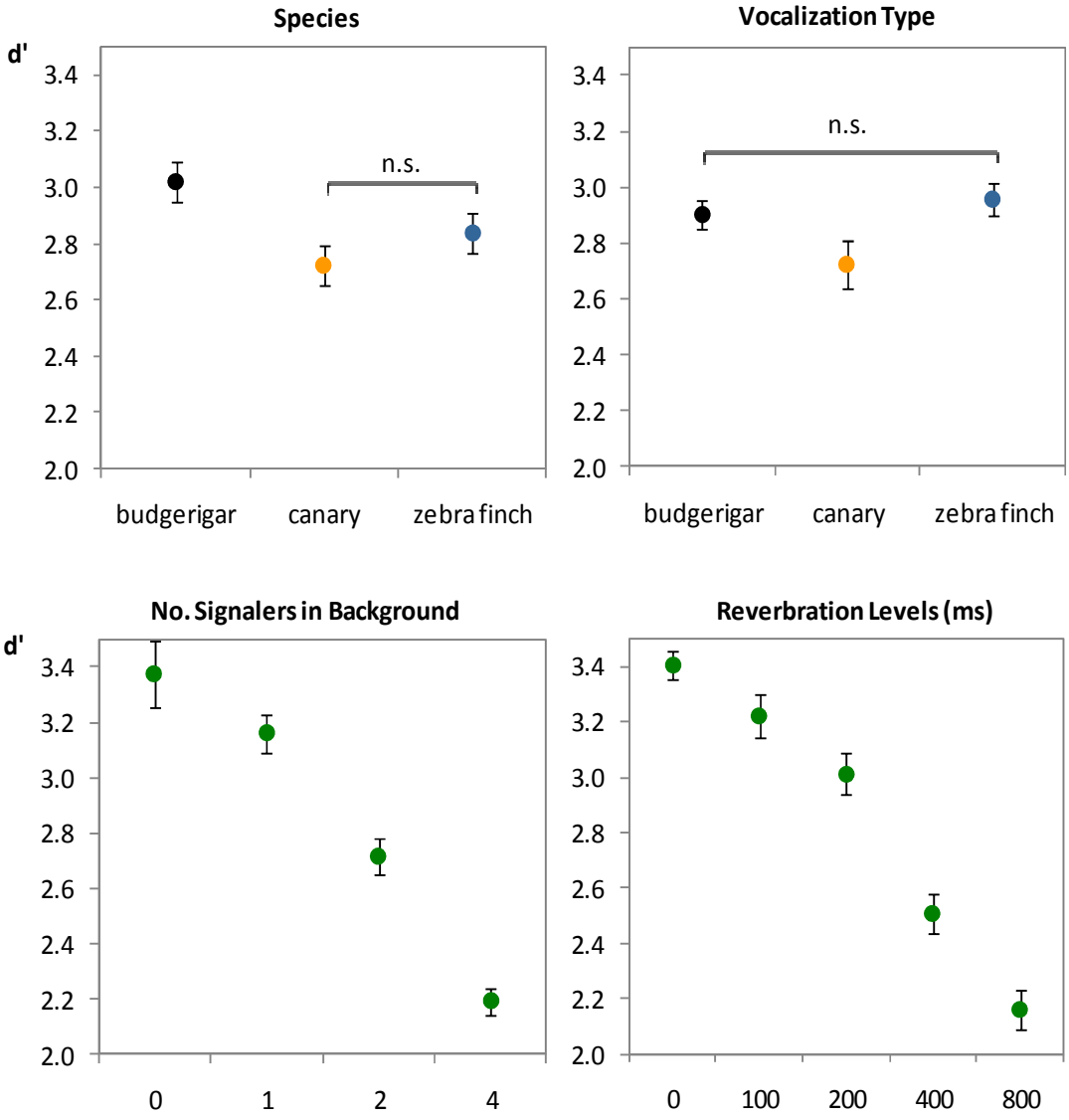


Figure 2. Main effects showing 95% Bonferroni-adjusted confidence intervals around estimated marginal means. Only non-significant differences between factor levels are marked (n.s.). Graphs illustrate the strong effect of both the number of signalers in the background and the reverberation level. As seen in other experiments, budgerigars again performed best and canaries worst. Budgerigar and zebra finch vocalizations with their broader frequency spectrum were also more easily detected and discriminated under all tested conditions than canary vocalizations.

a higher d' for all vocalization types, although this difference was significant only in the case of its own species' songs and those of the zebra finch (Figure 3 (a); SP x VT). In the latter case, however, the budgerigars and zebra finches performed almost equally well. Canaries, on the contrary, performed worse with all vocalization types than either of the other two species, although these performance differences were only significant when canaries were tested with budgerigar vocalizations (Figure 3 (a)). Only budgerigars and zebra finches were significantly better at hearing out and correctly discriminating their own species' song sequences. Differences in the species' performance as a function of reverberation level (SP x RL) were more apparent at medium reverberation times

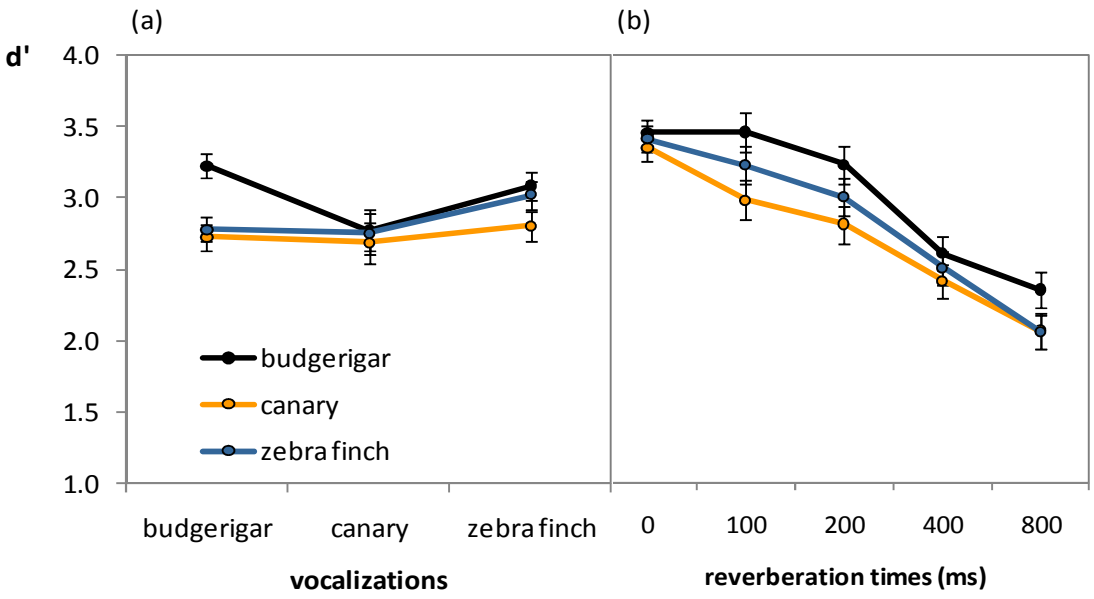


Figure 3. Interaction effect between (a) tested species and type of vocalization and (b) tested species and reverberation times (ms). Budgerigars had a significant advantage in tests with their own vocalization. Performance differences between species were negligible in tests with no reverberation but became significant at intermediate reverberation times. Bars represent Bonferroni-adjusted 95% CIs around estimated marginal means.

(100 and 200 ms) with budgerigars slightly outperforming the other two species and canaries having the lowest d' (Figure 3 (b)). Those species differences essentially disappeared at very low (or no) reverberation times (0 ms) and again at high reverberation times (≥ 400 ms). Figure 4 (a) illustrates the strongest interaction effect in the model, i.e. between reverberation time and number of background songs. It shows clearly that reverberation had a much greater negative effect on d' the more birds were singing in the background simultaneously.

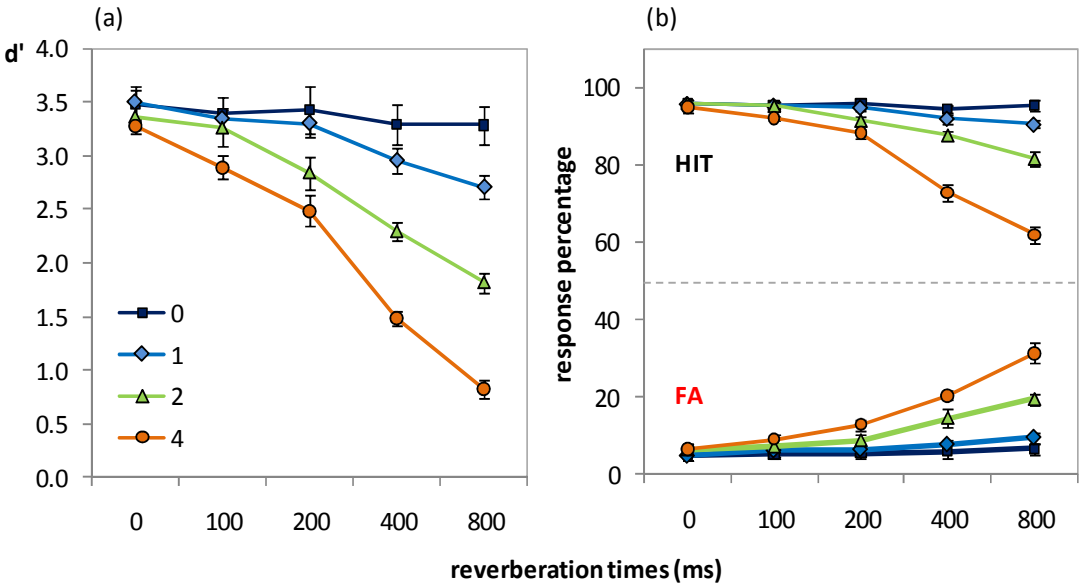


Figure 4. Illustration of the strong interaction effect between reverberation times (ms) and the number of individuals vocalizing in the background (0, 1, 2, 4). Effects on the birds' performance are shown for both (a) d' and (b) percentage of correct responses (HIT) versus false alarms (FA). (b) Indicates that the considerable drops in d' with increasing reverberation times seen in (a) were due to concomitant decreases and increases of hit and false alarm rates, respectively. Bars represent Bonferroni-adjusted 95% CIs around estimated marginal means.

The only significant third-order interaction effect on d' to which much of the data variation could be attributed was species x vocalization type x number of

background songs (η^2 = 0.673). Less abstractly speaking, the different species' performance depended significantly on the combined effect of vocalization type and number of songs in the background. Additionally, this combined effect had species-specific outcomes (Figure 5). For instance, budgerigars were the only species that performed worst with canary songs, especially in the presence of a background with multiple signalers. This effect is particularly strong for false alarm rates. The other third-order interactions, though significant, had negligible impact on the observed data variation (VT x BG x RL: η^2 = 0.282; SP x BG x RL: η^2 = 0.362; SP x RL x VT: η^2 = 0.288).

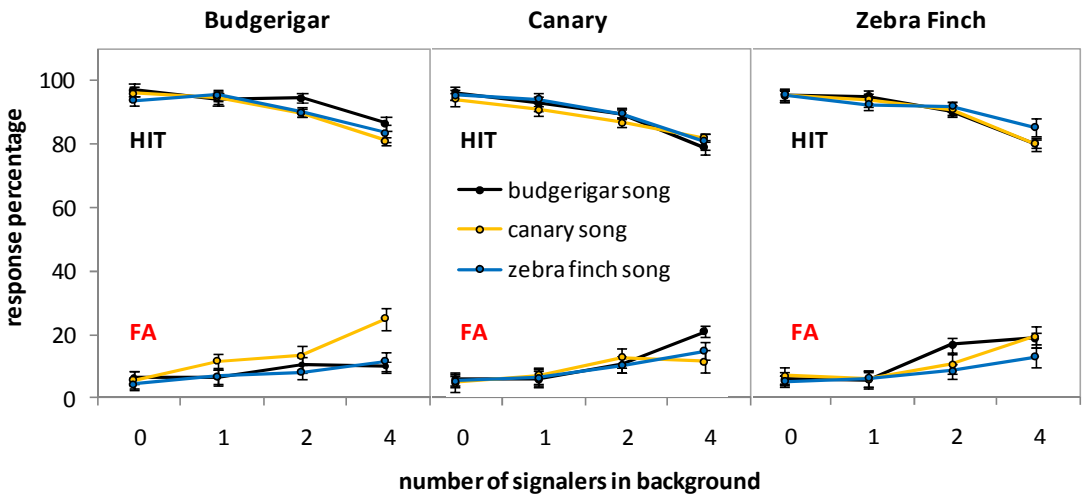


Figure 5. Interaction effect between vocalization type and the number of individuals vocalizing in the background (0, 1, 2, 4) shown for all species separately. Effects on the birds' performance are shown for percentage of correct responses (HIT) versus false alarms (FA). Differences in performance between vocalizations were reflected mostly in false alarm rates, especially when more individuals were signaling in the background. There is a slight tendency for each species to achieve somewhat higher % hits and lower % false alarms for their own vocalizations when the songs of at least two conspecifics were heard in the background. There is no such tendency with fewer or no individuals in the background. Bars represent Bonferroni-adjusted 95% CIs around estimated marginal means.

For proper evaluation of these results, certain d' values need to be explained in terms of less abstract measures of the birds' performance, which is why I provided some of the results as % hits and false alarms (Figure 4 (b) and 5). For a yes/no task similar to the one in this experiment, a d' of 1.0 is equivalent to 69% correct responses to either stimulus, i.e. 69% hits to GO stimuli and 69% correct rejections (or 31% false alarms) to NOGO stimuli across all trials (Macmillan and Creelman 1991, 2005). It can also be obtained for 50% hits, if false alarms are at about 16% across trials (see table in 2.2.5 "Measuring Auditory Sensitivities in the Lab"). It is clear from all graphs that the birds did very well in the majority of cases. Most performances lay well above a d' of 2.0. Sensitivities below this value of d' were only observed at a combination of high reverberation times (400 or 800 ms) and more individuals vocalizing in the background (2 or 4) (Figure 3 (a)) and can then reach values below 1.0.

The sensitivity index d' is an objective measure to account for variation in response proclivity across test subjects and conditions (see 2.2.5 "Measuring Auditory Sensitivities in the Lab"). However, in this type of experiment it can prove useful to analyze and specify potentially consistent changes across conditions. I first conducted a post-hoc uni- and multivariate Analysis of Variance with one between-subject factor and three repeated measures factors as described in "3.4.2 Methods", but this time using hit rate and false alarm rate as *two* dependent variables. This was to ensure that the overall statistical results did not differ greatly depending on the type of dependent variable chosen for analysis.

When compared with the results for d', this analysis confirmed that for both hit and false alarm rates all factors and interactions showed similar significance levels. Their relative contribution to the overall variation in the dataset was also unchanged for both hit and false alarm rates when compared with results for d', although changes in false alarm rates across conditions frequently contributed more than hit rates. Figure 3 (b) illustrates the concomitant changes of hit and false alarm rates for the strong second order interaction effect between reverberation level and number of signalers in the background. With increasing reverberation time and number of signalers in the background, correct responses to the GO stimuli decreased while false alarms to the NOGO stimuli increased, indicating a negative linear relationship between the two dependent variables. The results can be compared with the graph to the left showing results for d' (Figure 3 (a)). I then measured the strength and direction of the association between hit and false alarm rate by running a Pearson correlation analysis in SPSS (PASW Statistics 18, 2009) and found that there is indeed a highly significant negative linear correlation between the two variables (two-tailed test: $r = - 0.691$, $P < 0.001$, $N = 720$).

3.4.4 DISCUSSION

The major goal of this study was to investigate the effect of reverberation on behavioral measures of auditory object formation in a multi-signaler environment and to ask whether this effect is additionally dependent on the number of

signalers present in a reverberant environment. I further wanted to reveal any additional species-specific impacts, i.e. whether performance depends on the test species and/or the type of vocalization (conspecific vs. heterospecific). The way this study was designed, birds attended to one out of two complete vocalization sequences at a time and discriminated between them in the presence or absence of reverberation and simultaneous signalers. A complete object was formed if correct responses (GO or NOGO) were given to either of these two sequence. Since correct responses were only possible if the bird had listened to an entire 4-s sequence, a correct response also indicated that the auditory system had 'streamed' that sequence correctly.

Results from these psychophysical experiments showed clear independent effects of reverberation time, number of simultaneously singing individuals, and vocalization type on the formation of auditory objects. Most importantly, the birds' ability to selectively attend to a specific sequence of sounds was particularly compromised when very high reverberation times coincided with many birds singing in the background, indicating an interesting synergistic effect between the two factors. In contrast, neither of these factors alone ever decreased the birds' sensitivity to or below d' = 2.0, which means birds continued to do quite well on the discrimination task. There was a significant difference in the performance among the three species. In comparison with canaries and zebra finches, budgerigars had an overall easier time attending to a particular song sequence and discriminating it from others. This was true across all reverberation times and

across vocalization types. Only zebra finches and budgerigars achieved better performance for their own species' song, while canary songs were most difficult to follow and discriminate for all species including canaries. The vocalization effect, however, may not only be representative of the type alone but also the actual changes I introduced towards the end of all NOGO stimuli. As described in 3.4.2 "Methods", these changes differed across vocalization types (mostly temporal vs. spectral vs. compositional changes). In addition, although the selected test songs were all typical examples of the particular species' vocalizations, they by no means were representative of an entire population of a species' songs. Canary songs, for example, are quite varied and contain many syllable types. Trills, while exceedingly common in canary song, are made up of only one type that can be found in many variations. Therefore, results indicating somewhat species-specific performances (or the lack of it) do not necessarily tell us much about potential adaptations to a species' own songs. While this study does provide us with a first insight into potential species-specific adaptations, a larger variety of songs still need to be tested in the future.

In the present study, compromised auditory streaming was reflected by a decreasing hit rate accompanied by an increasing false alarm rate especially in conditions with extensive reverberation and a cacophony of songs in the background (see Figure 3 (b)). The Pearson correlation analysis clearly showed that this decline in performance as measured by these two variables can be expressed as a significant negative linear relationship between the two. In other

words, the more reverberation and simultaneous signalers, the harder it became to follow a particular song sequence toward the end in order to recognize it as either a GO or a NOGO sequence. Coherence of the tested sequences under non-reverberant conditions was likely due to the quick temporal succession of syllables (i.e. silent gaps of short duration), the syllables' common timbre that is specific to an individual, the natural order of syllables in the sequence, and their distinct temporal pattern of delivery with approximately equally long silent gaps between them. Reverberation essentially acts as a low-pass filter and any perceivable changes to a sequence's overall frequency should have been the same throughout and not have affected the sequence's perceived coherence. Reverberation effects on the aforementioned temporal characteristics of the sequence, however, may well have disrupted stream coherence to some extent. When performance dropped below sensitivity indices of 2.0 or 1.0 and decreasing hit rates resulted in concomitant increases of false alarm rates, it is possible that the birds had become incapable of actually integrating all elements of a song into a single stream and instead merely listened to an overall change in the background (i.e. the onset of a new sound). Since the sum of the percentage of hits and false alarm remained roughly the same across all conditions depicted in Figure 3 (b), it can be concluded that the ability to merely *detect* the presence of a song was unchanged, while the ability to perceptually *follow* and *discriminate* coherent sequences was significantly affected. The latter implies a perceptual deficit to some extent in the

birds auditory system to form coherent auditory streams in a highly reverberant 'cocktail party' environment.

In a cocktail party environment much like or acoustically more complex than the one I simulated in this study, informational and energetic masking from multiple signalers complicate auditory scene analysis and the effective formation of auditory objects (Brungart 2001; Brungart et al. 2001; Arbogast et al. 2002; Kidd et al. 2003; Arbogast et al. 2005). These effects can contribute to communication mistakes that may decrease fitness substantially, if neither the vocal production system nor the auditory system have evolved to adjust to or mitigate these constraints. If sensory information is to be used to control behavioral responses, the nervous system must be capable of making reliable perceptual judgments rapidly. It must have the capability of processing complex and constantly changing sensory information at once. This task is not always easy as sensory information sometimes presents conflicting or limited evidence about the environment. Nevertheless, the auditory system adheres to a set of perceptual principles that allow it to organize acoustic information into perceptually meaningful events, despite the lack of sensory evidence. If these rules are universal, then one could expect the auditory system to be sufficiently equipped with mechanisms (such as the use of binaural and spatial cues) that can make sense of an auditory scene with degraded signals. My results clearly suggest that although reverberation and the number of competing signals considerably decrease the ability to organize a cacophony of sounds into perceptually meaningful auditory objects, performance

largely remains at a level where communication is still possible (above chance). To be sure, the simulated 'cocktail party' is comparatively simple as it only contains a maximum of six different vocalizing individuals (four background songs plus one GO and one NOGO song) and reverberation times of up to only 800 ms. The results are nonetheless relevant and can add a missing piece in our knowledge of how the auditory system analyzes an acoustic scene by parsing relevant auditory streams from irrelevant sound sources.

Noise from multiple signalers is likely perceived as both *energetic* and *informational* masking. It seems plausible that *energetic* masking interferes with the audibility of different sounds by decreasing the signal-to-noise ratio of relevant sound sources, thereby simply removing or obscuring potential grouping cues. An increasing number of background songs also prevents birds from so-called 'dip listening' (e.g. Moore 1990; Eisenberg et al. 1995; Brumm and Slabbekoorn 2005; e.g. Fullgrabe et al. 2006) in the otherwise temporally fluctuating, abiotic background noise, because the composite waveform becomes more 'saturated' and contains fewer marked amplitude troughs of sufficient duration. This is further enhanced by the smearing, envelope-smoothing and masking effects of reverberation, which would explain the strong synergistic effect between number of background songs and reverberation level. Under these conditions it is further unlikely that common amplitude modulation patterns can be used as a grouping cue since amplitude modulations across the composite, multi-signaler waveform and the single songs are smoothed by reverberation and

masking effects. It remains open whether the fewer opportunities to listen in amplitude dips or the overall 'smoothing' of otherwise distinctive amplitude modulations are the main culprits. Further investigations with experiments specifically targeted at these questions are needed. It is probable that the aforementioned effects are combined with the fact that reverberations also obliterate sharp onset- and offset-times of sounds, diminishing the usefulness of these features as cues in object formation. Common spectral characteristics of sound components are also quite unreliable given that all songs are from the same species and therefore have similar frequency bandwidths and spectral patterns.

Informational masking, on the other hand, poses constraints on the cognitive aspects of auditory object formation that is steered by attention and requires rapid perceptual judgments based on the integration of large amounts of peripheral sensory information and prior experience (Durlach et al. 2003; Kidd et al. 2005). Given the apparently strong synergistic effect of reverberation time and numbers of simultaneous signalers, it can be speculated that the most severely affected cues are likely to be found where reverberation and masking effects from conspecifics intersect. Based on my discussion above, these cues are (but may not be limited to) center frequency or modulation patterns, amplitude fluctuations, envelope coherence across frequencies, common onset- and offset times, and – possibly – timbre.

In conclusion, the present study has provided evidence that auditory stream segregation occurs in three bird species that have not been tested in this

fashion before. More importantly, it revealed that in a cocktail party environment with multiple signalers, sound reverberation plays a critical role in affecting the percept of distinct auditory objects or streams and renders identification of individual sound sources more difficult. The degree to which auditory stream segregation is compromised depends on the amount of reverberation as well as the number of signaling individuals. In this study, I only investigated a limited range of possible combinations of different sounds and reverberation times, and as such the conclusions that can be drawn from it are, of course, limited. In the future, other naturally occurring songs and various combinations of differentially reverberated background and target sounds could be used. Moreover, this study focuses primarily on natural vocalizations, since my primary interest was to understand the effects of reverberation on the perception of long sequences of typical bird songs in a multi-signaler environment (or Cocktail Party). Subsequent studies could succeed in disseminating specific effects of reverberation on particular grouping cues in more controlled experiments by using specifically designed artificial stimuli and modified natural vocalizations.

My experiment was further designed to attempt a behavioral approach in answering the question of whether birds are capable of selectively attending to and following a long sequence of sounds that originate from a specific sound source while segregating it from others. There has been a reluctance to investigate this aspect of auditory scene analysis (ASA) behaviorally in animals, because it is deemed difficult to determine whether the auditory system in fact

attends to and segregates complete sequences of sounds based merely on behavioral responses of the test subjects. In fact, as of today there is hardly any behavioral study published in peer-reviewed journals that has successfully and unequivocally tested auditory object formation in animals using a purely psychophysical paradigm. The current study describes a feasible approach that may mitigate some of these concerns and provide a useful basis for future refinement of the proposed methodology in investigations concerning auditory object formation or stream segregation.

4 CONCLUDING REMARKS

This dissertation describes a series of behavioral laboratory experiments that were designed to examine the perception of reverberation effects on acoustic signals. The experiments centered on four major research questions that are listed (with sub-questions) in 2.1 “Outline and Objectives”. My findings indicate that the birds’ extraordinary sensitivity to reverberation differences (1) and their ability to categorize reverberation times across stimuli (2) allows for reverberation to be used as a cue in the evaluation of signaler distance or the acoustic properties of the environment, especially when masking from noise is low. The experiments also showed that very high levels of reverberation, particularly in combination with noise, severely affect vocally-mediated discrimination of individuals with similar vocalizations (3), which may be problematic for species with high levels of song sharing or other forms of vocal mimicry. Moreover, in multi-signaler environments reverberation can interfere with auditory stream segregation (4), which allows receivers to perceptually parse a complex acoustic scene by segregating relevant from irrelevant sound sources and thereby facilitates selective attention to sequences of coherent sounds. The results suggest, however, that a bird’s ability to segregate an individual’s vocalizations from a cacophony of other songs is significantly hampered only at very high reverberation times and with at least four simultaneous signalers in the background, a condition that is commonly encountered in social groups or networks that inhabit reverberant environments, such as forests. A common pattern in all the findings

reported in this dissertation is the rather consistent difference between divergent bird taxa (i.e. the tested psittacine and oscines) in their performance under reverberant and noisy conditions, with the budgerigar as the only non-songbird retaining the greatest perceptual sensitivity. Budgerigars and zebra finches with their extraordinary spectral and temporal resolving power, respectively, were rather similar in their ability to perform various tasks under these conditions. These results somewhat contradict the viewpoint that species-specific adaptations of the auditory system exist as a result of distinct selective pressures arising from intraspecific communication in particular habitats. Instead, one may speculate that the ability to both utilize and cope with reverberation, even in noise, may be reflective of its fundamental adaptive value for any vocally communicating individual rather than being a specialization. If this is true, then other vocal species, too, should have broadly similar capacities, because reverberations and noise are ubiquitous and should therefore constitute problems that are common among all these animals.

Overall, I was able to show that when reverberation and noise levels are high, reverberation has the potential to remove information contained in a signal, while noise masks it – both of which ultimately affect the transfer of information and message decoding. From a behavioral ecology viewpoint, however, the combined debilitating effects of noise and reverberation are likely less severe in natural habitats due to both behavioral strategies and sensory mechanisms that take effect in species-typical listening situations and environments in the wild. For

instance, perception can be enhanced by changing receiver positions relative to the sound source and reflective surfaces, using multimodal signals if available, and relying on perceptual mechanisms that enhance signal detectability and intelligibility, such as spatial release from masking, which does not occur if noise is emitted from a single source (i.e. a speaker). Investigating reverberation effects in the field could therefore give some valuable insight into the role of these strategies and mechanisms in alleviating the compromising effects of reverberation and its interaction with noise. This is important if the aim is to evaluate more precisely the fitness consequences that arise from communicating in reverberant, noisy environments. However, one should bear in mind that, even if reverberation can be dealt with in the wild or at moderate levels in the laboratory with relatively little masking from noise, increased masking from artificial, *anthropogenic* noise sources can negate some of the current sensory adaptations. In such cases, fitness consequences arising from communicating in complex reverberant environments may in fact be severe and affect species conservation (see e.g. Popper 2003; Slabbekoorn and Ripmeester 2008). There is evidence to suggest that, at least in humans, perceptual performance in noise alone cannot predict the perceptual difficulty a listener may encounter when reverberation and noise are combined (Nabelek and Mason 1981). Therefore, identifying anthropogenic noise sources and their loudness in specific habitats and subsequently testing the affected species in the lab with a combination of this noise and habitat-typical reverberation may offer a more complete picture of how

well species are adapted even to unnatural conditions like these, and whether reverberation effects are in fact enhanced.

In addition, investigating how reverberation affects signal processing at a neuronal level would help understand the underlying physiological mechanism for the relative salience of signals under reverberation and the combined effects of reverberation and noise. Incidentally, at signal frequencies below about 5 kHz, information about both the amplitude modulations of a signal *and* its spectral features is encoded by the temporal firing pattern of auditory neurons on the basilar membrane. This temporal coding of low frequencies has shown to be particularly resistant to masking from noise in several species (Gleich and Narins 1988, Ratnam and Feng 1998), and could also prove to be of particular importance for overcoming reverberation effects in natural environments.

APPENDIX I

Conversion of hit rate and false alarm rate into d' (dprime)

Calculations of d' were based on computation examples given in Macmillan and Creelman (1991, Appendix 6). Part of the routine is the computation of z-scores, which can only be achieved by approximation. The approximation used here has been assessed to be the most accurate when compared to other competing methods (Brophy 1985). Data frequencies of 0 or 100%, i.e. proportions (p) of 0 or 1, cannot be calculated and need to be converted to 1/(2N) and 1 – 1/(2N), respectively, because they otherwise would result in infinite values. N represents the number of total trials that a stimulus was presented. I executed the computations in Microsoft Office Excel 2007, to which I provided simple stepwise instructions below. These steps should be easily convertible into other programming languages.

```
hitrate :=  p(hits)

farate := p(false alarms)

y1 := SQRT(-2*ln(hitrate))

y2 := SQRT(-2*ln(farate))

z(hitrate) :=  – y1 + ((((0.0000453642210148 * y1 + 0.0204231210245) * y1 +
0.342242088547) * y1 + 1)
* y1 + 0.322232431088) / ((((0.0038560700634 * y1 + 0.10353775285) * y1 +
0.531103462366) * y1 + 0.588581570495) * y1 + 0.099348462606)


z(farate) :=  – y2 + ((((0.0000453642210148 * y2 + 0.0204231210245) * y2 +
0.342242088547) * y2 + 1)
* y2 + 0.322232431088) / ((((0.0038560700634 * y2 + 0.10353775285) * y2 +
0.531103462366) * y2 + 0.588581570495) * y2 + 0.099348462606)

z1 := z(hitrate)

z2 := z(farate)

dprime := z1 – z2
```

APPENDIX II

Algorithm for Artificial Reverberation Implemented in Matlab 7.5.0 (The Mathworks Inc. 2007)

(Courtesy of Mounya Elhilali)

```
function [y,h,Fs] = add_reverb(data,Fs,reverbTime,method,extendLen)  % adds
reverberation to waveform

if nargin < 3
   error ('Must include at least three parameters');
end

if ischar(data)
   [data,Fs] = wavread(data);
end

if isempty(Fs) || Fs <= 0
   error ('The sample rate Fs must be larger than zero');
end

if nargin < 4 || length(method) ~= 1 || ~isnumeric(method)
   method = 1;
end

if nargin < 5 || length(extendLen) ~= 1 || ~isnumeric(extendLen)
   extendLen = 1.0;
end
n = round(extendLen*Fs*reverbTime);

if n <= 0    % No reverberation to be done
   y = data;
   h = 1;
   return
end

data = [data(:) ; zeros(n,1)];
alpha = 3*log(10) / (2*Fs*reverbTime);

switch method
case 1
   h = randn(n,1) .* exp(-alpha*(0:n-1)');
case 2
   h = 2*(rand(n,1)-0.5) .* exp(-alpha*(0:n-1)');    % h = 2*(rand(n,1)-0.5);
case 3
   h = exp(-alpha*(0:n-1)');
otherwise
   error ('Unknown method "%d"',method)
end

h = h ./ sqrt(sum(h.^2));    % h = max(h, 0);
y = fftfilt(h,data);
return
```

Parameters:

data = Input waveform. This can also be a filename, which is read using wavread(). In this case, Fs is set from the file.

Fs = Sample rate of the waveform (Hz).

reverbTime = Exponential decay time of the intensity (seconds).

method = Method to use for adding reverb

1 = Design exponentially decaying impulse response using Gaussian noise. Convolve using fftfilt().
2 = Design exponentially decaying impulse response using uniform noise. Convolve using fftfilt().
3 = Design exponentially decaying impulse response without noise. Convolve using fftfilt().

extendLen = This is the amount of time, in units of reverbTime, of silence added to the input sound before convolving. This amount of time allows the sound to decay away. Setting this to less than 1.0 will chop off the sound at the end.

Defaults:
method = 1
extendLen = 1.0

Method 1 (exponentially decaying impulse response using Gaussian noise) was used to convolve the original, non-reverberated stimuli.

APPENDIX III

Algorithm for Envelope Extraction and Imposition on Generated Non-Random White Noise Implemented in Matlab 7.5.0 (The Mathworks Inc. 2007)

```
function Fs = make_env_nonrand_noise_files(prefix, suffix)
% Usage: make_env_noise_files( prefix, suffix )
%      prefix: prefix string for calculating filename
%      suffix: suffix string for calculating filename
% Process a set of signal files.  For each file:
%    1. Read file
%    2. Extract envelope
%    3. Impose envelope on random noise signal
%    4. Write envelope-impoesed noise signal to new file.
%
% Returns: Fs, the sampling frequency read from final input wav file.
%
% Example:
%    Fs = make_env_noise_files( 'zf 2 rev ', ' ms' )
%
% Author: David Eisner & Sandra Blumenrath

Fprintf ( 'Prefix: %s\n', prefix );

% Reverb delay times:
%   Start with 0ms up to 10ms in increments of 1ms
%   then           up to 100ms in increments of 10ms
%   then           up to 200ms in increments of 50ms

delays = [0,1,2,3,4,5,6,7,8,9,10,20,30,40,50,60,70,80,90,100,150,200];

for i=1:length(delays)

    in_fname = sprint ('%s%d%s', prefix, delays(i), suffix);
    fprintf ('Reading file: "%s"\n', in_fname );

    [y, Fs] = wavread( in_fname );
    env_y=envelope (y);
    L=length(y);

    randn ('state', 89)
    % randn(method,s) causes randn to use the generator determined by method, and
    % initializes the state of that generator using the value of s. (method:
    % 'seed'; here, seed is set to 89 for creation of non-random noise
    total_89 = randn(L, 1);
    to1 = 0.001;
    total_89_b = total_89 * ((1-to1) / max(abs(total_89)));
    % y_seed_89 = total_89_b (1:size (env_y));
    % final_y_seed_89 = env_y *y_seed_89;
    final_y_seed_89 = env_y .* total_89_b;

    out_fname = sprint ('nr_envn_%s%d%s', prefix, delays(i), strtrim(suffix));
    fprintf ('Writing file: "%s"\n\n', out_fname );
    wavwrite (final_y_seed_89, Fs, 32, out_fname);
end
```

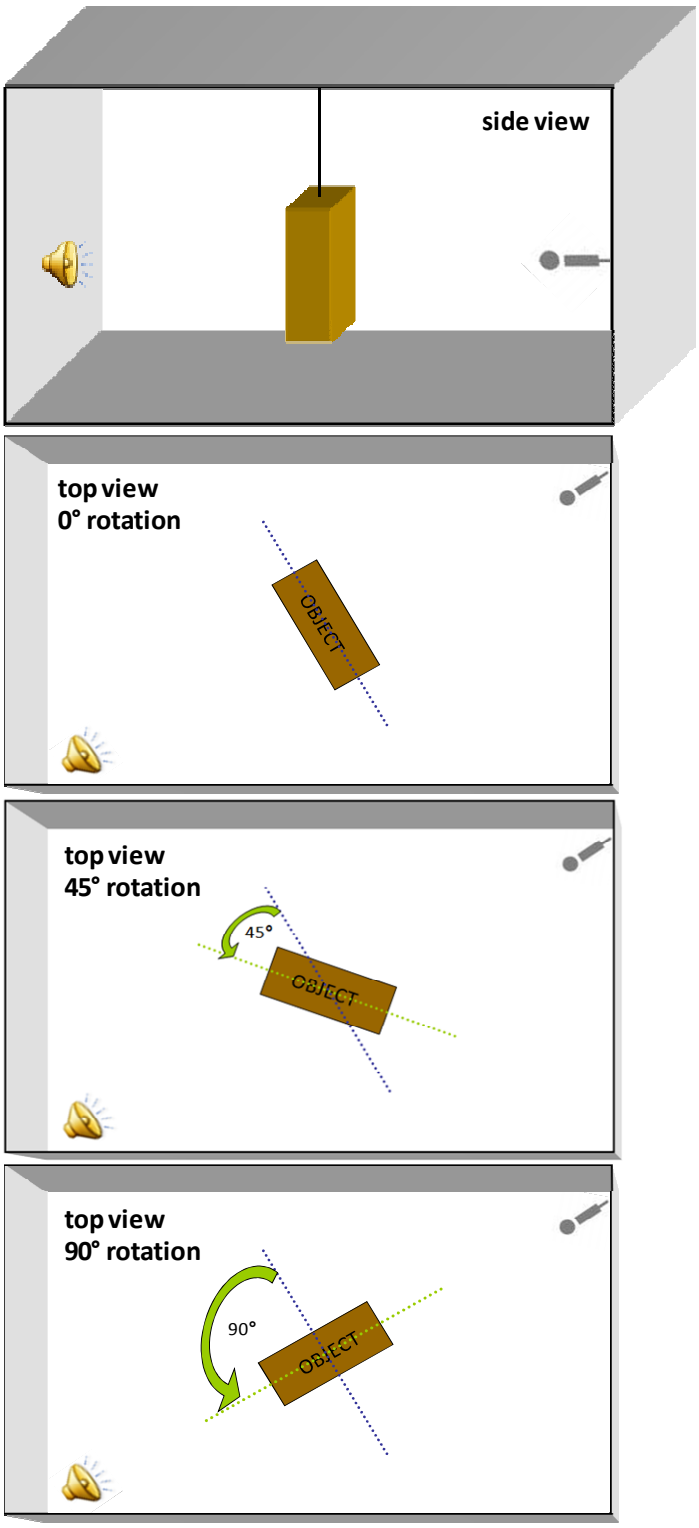
Random noise alone is generated by the following modified code section taken from above:

```
randn ('state', s)
total_rand = randn(L, 1); % L is the desired length or duration in samples of the
generated noise
    to1 = 0.001;
    total_rand_b = total_rand * ((1-to1) / max(abs(total_rand)));
end
```

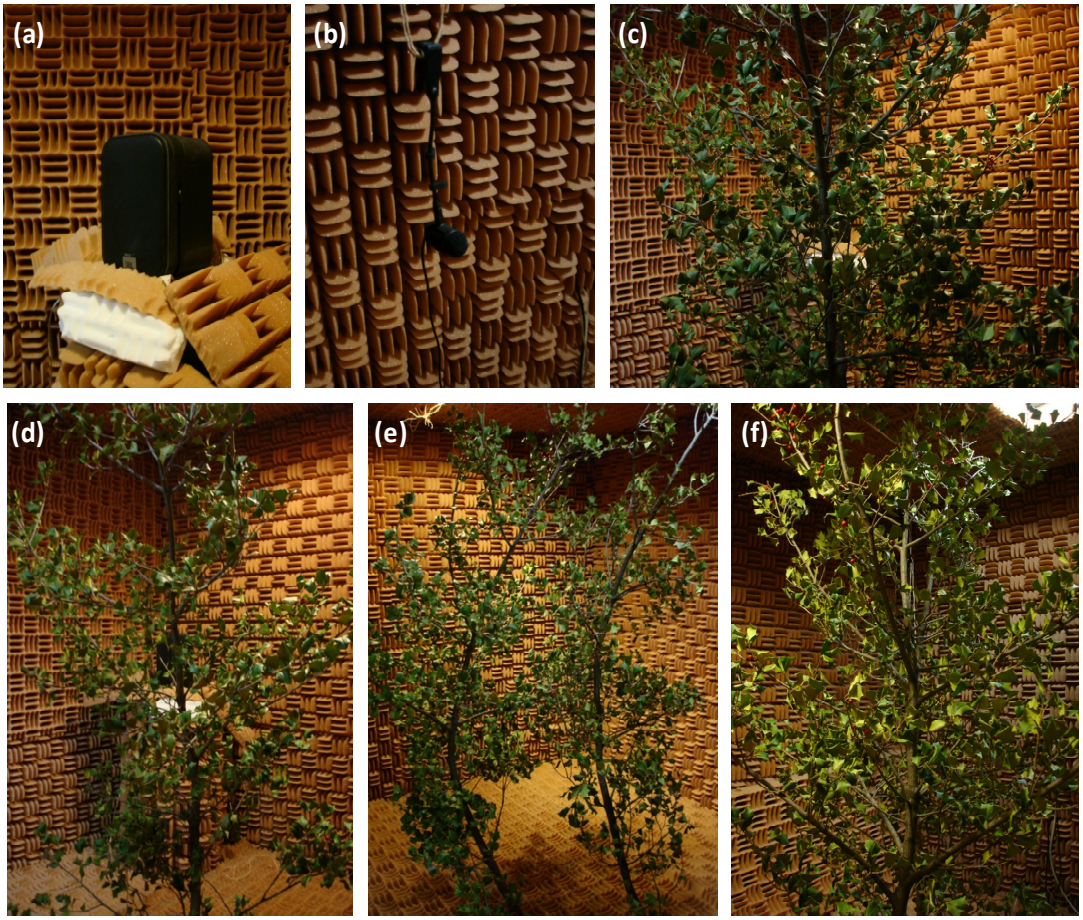
APPENDIX IV

Acoustic Chamber Setup

(a) Variation in Object Position (Cardboard Box)

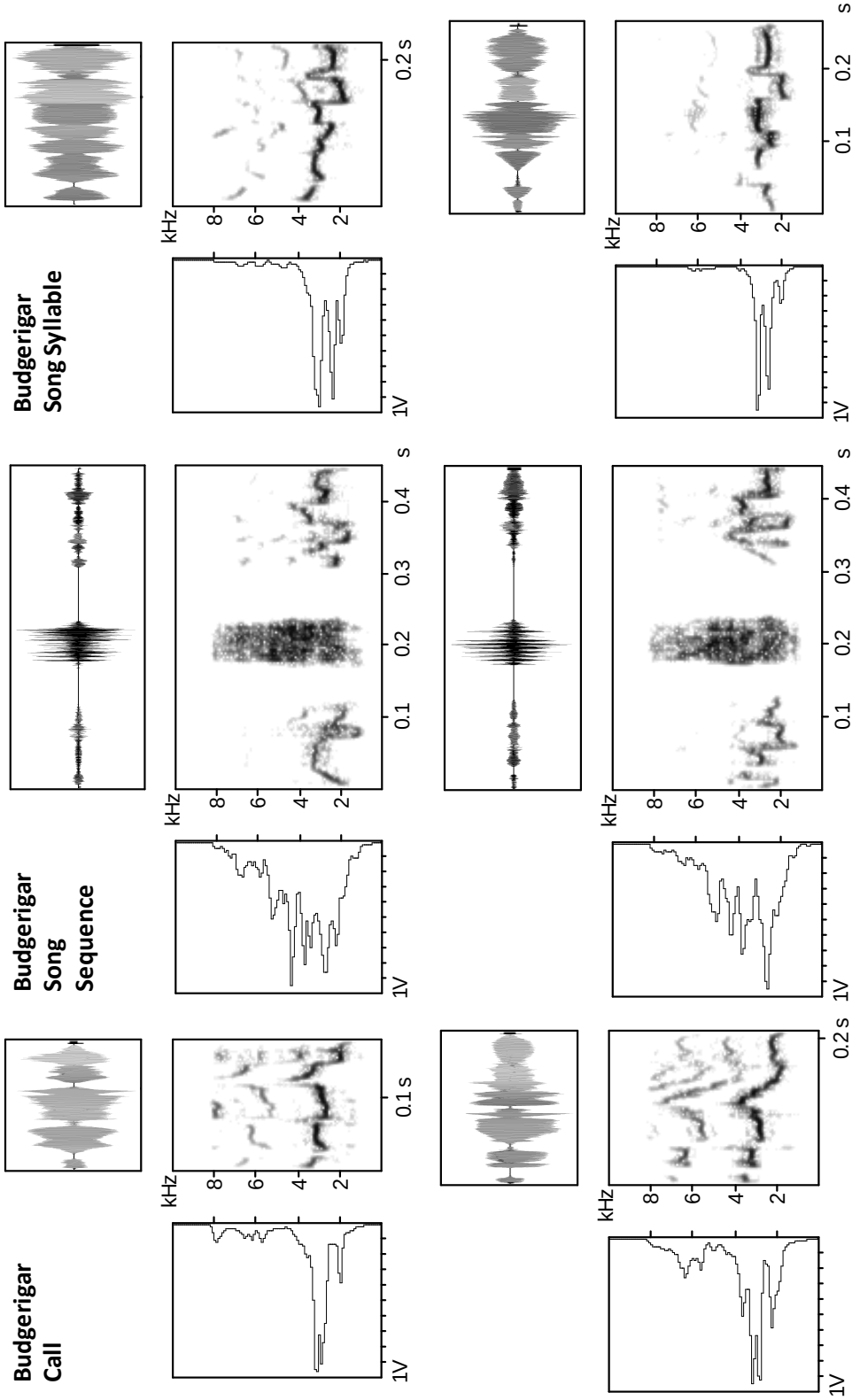


(b) Holly Tree Branches

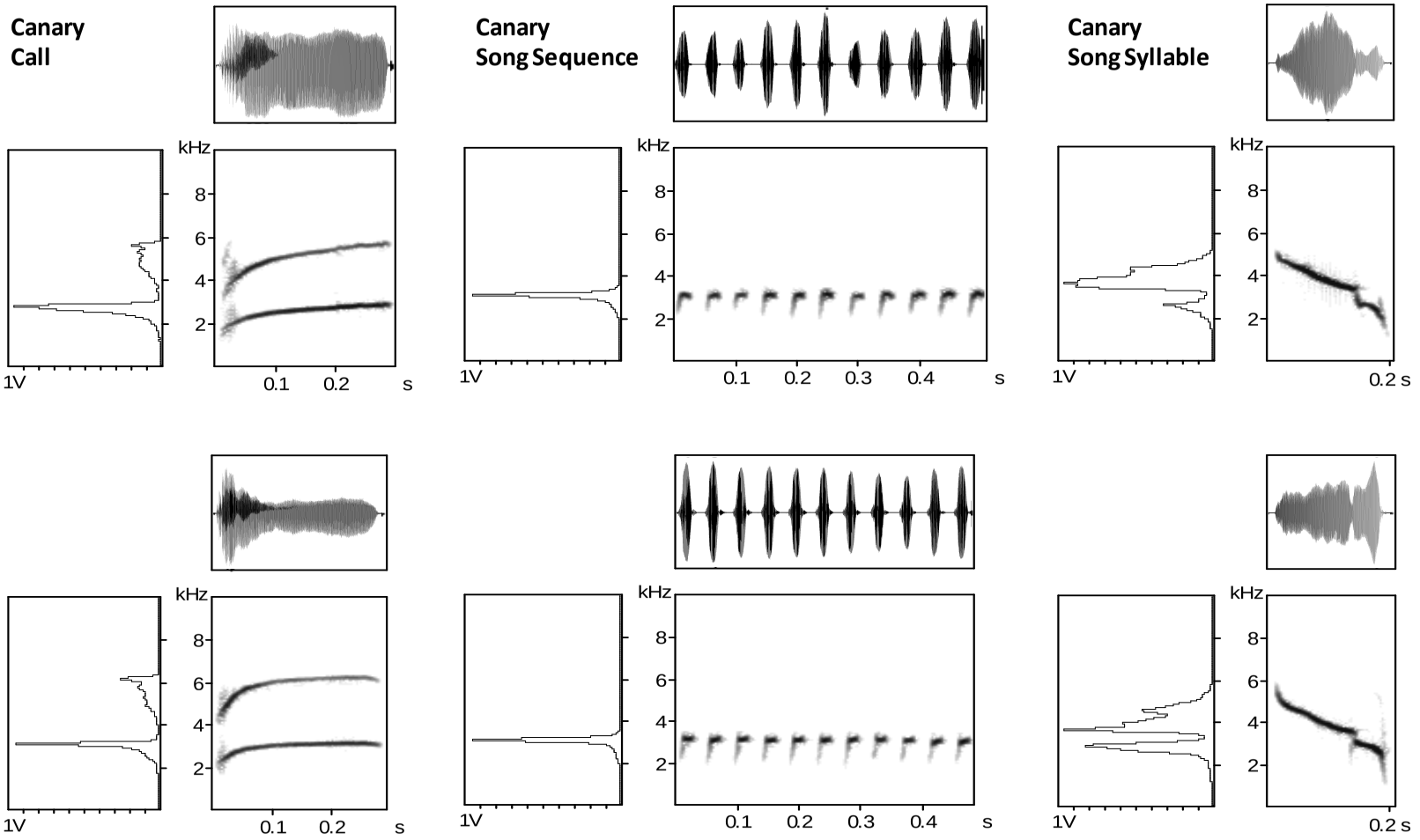


(a) Speaker on sound-foam-padded pedestal
(b) Free-hanging microphone
(c) Branches, microphone perspective
(d) One branch, microphone perspective
(e) Two branches, side view of transmission pathway (not visible: speaker to the left, microphone to the right)
(f) One branch, speaker perspective
(g) Two branches, microphone perspective

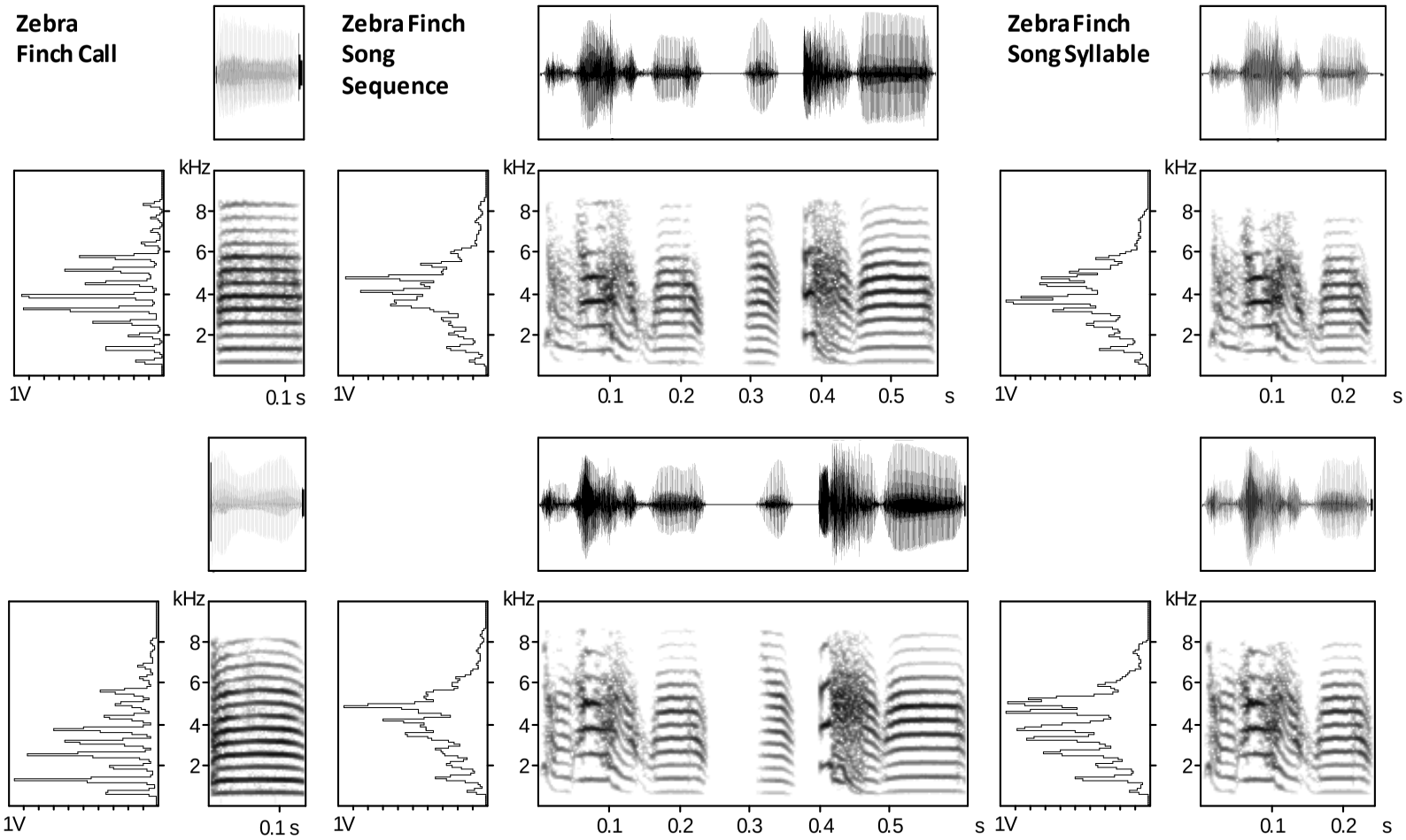
APPENDIX V



Non-reverberated pairs of similar budgerigar vocalizations from different individuals: contact calls, excerpts from songs (or warbles), and single song syllables. Stimuli of a pair are positioned underneath each other. Spectrogram (middle), oscillogram (top) and frequency spectrum (left) are sown for each vocalization.



Non-reverberated pairs of similar canary vocalizations from different individuals: contact calls, excerpts from songs, and single song syllables. Stimuli of a pair are positioned underneath each other. Spectrogram (middle), oscillogram (top) and frequency spectrum (left) are sown for each vocalization.



Non-reverberated pairs of similar zebra finch vocalizations from different individuals: contact calls, excerpts from songs, and single song syllables. The song excerpt constitutes a complete motif that is repeated throughout the song. Stimuli of a pair are positioned underneath each other. Spectrogram (middle), oscillogram (top) and frequency spectrum (left) are sown for each vocalization.

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